Systematic Zoology

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The Name *Psammochares* versus *Pompilus*

HENRY TOWNES

IN CONNECTION with a monograph of some Nearctic spider wasps, I recently had occasion (1957, *Bull. U. S. Nat. Mus., 209*:2-3) to discuss the choice between Psammocharidae and Pompilidae as the proper scientific name for the family, which names are based on the generic names *Psammochares* Latreille, 1796 and *Pompilus* Fabricius, 1798. Professor J. Chester Bradley has published an article (1957, *Syst. Zool., 6*:101-106) criticizing the views expressed there. My taxonomic paper gave only a statement of my general position, but with the publication of Bradley's article there is reason to go into more detail.

Bradley and I are of opposite views on the desirability of *nomina conservanda* as administered by the International Commission on Zoological Nomenclature, and this is the cause of the disagreement brought out in Bradley's article. It happens, however, that the International Commission has never made a *nomen conservandum* of *Pompilus*, even though Opinion 166, on which Bradley has based his argument, presumes that it did. If it can be shown that Opinion 166 is spurious and not valid, it automatically follows that Bradley's view is not valid under the International Rules and Opinions, and that the only question remaining is whether an appeal to the Commission to make a new, valid, Opinion favoring *Pompilus* over *Psammochares* would be in the interests of sound and stable nomenclature. This legalistic approach was not taken in my earlier discussion because I considered that the nomenclatural questions had been settled more than a century earlier than Opinion 166, by the original proposals of the names and selection of their genotype *. According to this view any subsequent action is quite irrelevant, regardless of involved discussions or legal phraseology, and the only reason for going into the validity of Opinion 166 would be the practical importance of bringing agreement on a scientific name, even if by different routes of reasoning.

Most of the nomenclatural facts on the *Psammochares-Pompilus* question were thoroughly discussed by Pate in 1946 (*Trans. Amer. Ent. Soc., 72*:123-128). His conclusion was that the genotype * of *Psammochares* is *Sphex fusca* Linnaeus (designated by Latreille, 1803) and that the genotype * of *Pompilus* is *Pompilus viaticus* Fabricius, which is the same as *Sphex viatica* Linnaeus (designated by Latreille, 1810). Neither Bradley nor I disagree with Pate's conclusions on the genotype * of these two names under the International Rules of Zoological Nomenclature. Our disagreement centers on Opinion 166 of the International Commission which is rejected by Pate and me but accepted by Bradley. Opinion 166 proposes, under "suspension of the rules" of nomenclature, arbitrarily to suppress *Psammochares* and to change the designated genotype * of *Pompilus* from *Sphex viatica* (a sphecid) to *Pompilus pulcher* Fabricius (a psammocharid). My reason for rejecting this Opinion, regardless of the question of its authenticity,

* It is the express wish of the author to use "genotype" rather than "type species" throughout this paper. *Ed.*

was that it advocates violation of well-established rules of nomenclature and general standards of accuracy and consistency, and that by violation of these cornerstones of good nomenclature it has a harmful influence on the whole system greater than any good that could be accomplished by conserving a particular name. Bradley's position seems to be that no zoologist should use his personal judgment in opposition to the International Commission, and that the names of all animals, to be correct, must agree with the Opinions of the International Commission.

Bradley's case for *Pompilus* therefore rests on the authenticity and validity of Opinion 166. This Opinion involved a "suspension of the rules" of nomenclature for a scientific name which was represented as being worthy of this exceptional treatment. The International Commission was given power to make *nomina conservanda* under "suspension of the rules" by the International Congress of Zoology, meeting in Monaco in 1913. To control the use of this power and to prevent its abuse, it was stipulated that certain procedures had to be followed. The required procedures, as first published by the Monaco Congress, and repeated in later publications, are: (1) Publication in certain journals that the case is under consideration. (2) A wait for at least a year to give the scientific public opportunity to submit arguments for or against the proposal. (3) A vote by the commissioners. If the vote is unanimous, the proposal is approved. If less than unanimous, but at least a two-thirds majority of the full Commission, the case should be reported to the next succeeding International Congress of Zoology for disposition under a stipulated procedure. This latter step, however, was not taken for Opinion 166 so is of no concern here.

In comparison with the required procedures, the history of Opinion 166 is as below. All of the facts except the letter from Peters, and protests that were sent to the Commission on the illegality of its action in Lisbon, are in published records where they can be checked.

1928. Circulation of a petition by Bradley that *Psammochares* be suppressed and that *Sphex viatica* Linnaeus be considered the genotype * of *Pompilus*. The petition and the list of persons signing it are reproduced in Opinion 166, page 378.

1935. The Commissioners' meeting in Lisbon at the International Congress of Zoology decided to consider Bradley's petition, which then had the genotype * proposed for *Pompilus* emended to *Pompilus pulcher* rather than the original *Sphex viatica*. Six of the sixteen regular Commissioners were present in Lisbon; six others were selected as temporary substitutes (among them Professor J. Chester Bradley) for some of the missing regular commissioners. Ten of these twelve were present when the vote on Opinion 166 was taken. (See the minutes of the Lisbon Congress.) Following news of this vote on *Pompilus* (and other names of Hymenoptera in the same list), protests were sent to the Commission that it had not published the proposal before the vote, to allow for arguments for or against it by the scientific public, as a result of which no deciding vote could have been taken.

1936. The proposal was published and the scientific public invited to send arguments for or against it.

1937. The following are the comments received by the Commission (see Opinion 166, pages 382-383):

From S. A. Rohwer (opening paragraph giving nomenclatural data omitted):

Since Banks, 1910 (Jour. N. Y. Ent. Soc. vol. 18:114), called attention to the fact that *Psammochares* Latr. has priority over *Pompilus* Fabr., the principal workers in the family have employed the name *Psammochares* for the genus. Included among these are Banks, Haupt, Arnold, Gussakovsky, Nielsen, Grandi, Turner, Williams, Brèthes, Bernard, Maréchal, Richards, and Sustera. During this period the name *Pompilus* has virtually appeared only in connection with scattered biological notes. To

reject now the prior *Psammochares* Latr. in favor of the subsequent *Pompilus* Fabr. would result in overturning the nomenclature of the group which has been nearly uniform for the past twenty-five years, during which time more progress has been made in the taxonomy of this family than in any other similar period.

In this case only confusion can result from the proposed action under suspension of the rules.

From C. D. Michener:

Pasmmochares is the name now in use and is correct without a suspension of the rules.

1939. Karl Jordan and Francis Hemming met the evening of June 19. These two Commissioners decided that the case of *Pompilus* should be concluded and agreed between themselves that the communications from Rohwer and Michener brought forth no new considerations, and that an Opinion should be issued putting into effect the vote made in Lisbon in 1935. As authority for their action it has been stated that on adjournment, the Lisbon meeting authorized the president (Jordan) and incoming secretary (Hemming) to "take such action as might appear to them necessary or expedient . . . to give effect to the decisions reached by the Commission at the Lisbon session. . . ."

1943 (March). I wrote to James L. Peters, one of the Commissioners and Acting Secretary of the Commission at the Lisbon congress, inquiring about whether any action had been taken, or was contemplated, on the names of Hymenoptera brought up at the Lisbon meeting. At that time my interest was in the names *Ephialtes, Ichneumon,* and *Pimpla,* which were on the same list as *Pompilus* before the Commission and had exactly the same history in the Commission. (Hemming, Secretary of the Commission, was believed not available to answer letters, because of war conditions.) Peters' answer was as follows:

After receiving your letter of March 22nd I went through my entire file of Circular Letters from the Secretary (both past and present) of the International Commission on Zoological Nomenclature and cannot find that the question of the suspension of rules in favor of the genera *Ichneumon, Pimpla,* and *Ephialtes* was ever circulated. Notice that suspension had been requested was published in several zoological journals in 1936 and action could not have been taken before 1937, since one year is required to lapse in order to give the interested parties time to present arguments for and against suspension.

Anyway no vote has been taken on the subject of these three names and I think it would be very wise if you proceeded to apply the names in accordance with the accepted international rules since it cannot be until after the war that the question of suspension can be put to a vote and of course no one knows then how the vote would stand.

1943 (October). The results of the meeting between Jordan and Hemming in 1939 were published by Hemming in the Bulletin of Zoological Nomenclature (*1*:77).

1945. Opinion 166 was published.

The record shows that the question of *Pompilus* was never voted on by more then ten of the Commissioners, so could not have had a unanimous vote. Moreover, any vote to be valid would have to have been taken a year *after* publication of the proposal, and in light of whatever arguments for or against the proposal were received from the scientific public. Jordan and Hemming thought that Rohwer's and Michener's protests contained nothing which might affect a vote if it were called for, but what more important could Rohwer and Michener have stated than that *Psammochares* was already in well-established usage and should not be changed? At any rate, regardless of the opinions of Jordan and Hemming, no vote was either asked for or received from the other Commissioners after publication of the proposal in 1936. The direction on adjournment of the Lisbon meeting of the Commissioners to Jordan and Hemming to put into effect the decisions of the meeting did not give Jordan and Hemming power to *make* the decisions, and even if it did they could not have decided the case of *Pompilus* be-

cause this proposal was never legally the business of the Lisbon meeting.

Opinion 166 (and a number of others with a similar history) is therefore spurious and without validity. This leaves the alternatives of using only *Psammochares* and Psammocharidae or (for persons using *nomina conservanda*) of making a new request to the International Commission for official approval of the proposal to conserve *Pompilus* and Pompilidae. If there is now (1958) approximately equal usage of *Psammochares* and *Pompilus,* or greater usage of *Psammochares,* there would seem no reason for the Commission to make a *nomen conservandum* of *Pompilus,* and no reason for any one to request it unless his personal "prestige and convenience" were involved.

The basic literature on the family may be listed as follows, these being the works comprehensive enough to be widely known and consulted, and not likely to be replaced by new papers in the near future:

HAUPT, 1927. Monograph of the European species.

ARNOLD, 1932–36. Monograph of the Ethiopian species.

BANKS, 1934. Monograph of the Philippine species.

EVANS and BRADLEY, 1944–51. Monograph of one subfamily of Nearctic species.

PATE, 1946. A list of the genera of the world, with their genotypes.

BANKS, 1946–47. Monograph of the South American species.

TOWNES, 1957. Monograph of two subfamilies of Nearctic species.

Of the above, only the papers by Evans and Bradley use *Pompilus* and Pompilidae in preference to *Psammochares* and Psammocharidae. A tabulation of the smaller papers produced by the last generation of workers would show that *Psammochares* and Psammocharidae are used about as frequently as *Pompilus* and Pompilidae, with possibly a preponderance of the former pair of names in the more technical papers. In the face of this, it would hardly be justified for the International Commission to "suspend the rules" in favor of *Pompilus* and Pompilidae.

If we agree that *Pompilus* can be used only in the Sphecidae and that *Psammochares* remains a valid name for a genus of spider wasps, we come next to the question of whether Psammocharidae as used by Banks, Haupt, Arnold, Pate, myself, and others or whether Aporidae as contended by Bradley, is the correct name for the family. If the oldest genus of the family is used as the basis for the family name, Psammocharidae is correct, but if the genus which was first pluralized to form a supergeneric group-name is used as the basis for the family name, Aporidae appears to be the correct one. These are opposing ideas and there is no firm precedent for deciding between them. The Strickland Code (1842) and the Dall Code (1877) suggest, among other things, the use of the oldest generic name. The International Code (1901) evades the question and some attempts to get a ruling from the International Commission on the matter have resulted in non-committal statements like that of the Lisbon (1935) meeting . . . : "Article 4 of the Code, which relates to the naming of families and subfamilies, *does not require* that the oldest generic name in the family or subfamily concerned *must* be taken as the type genus of the family or subfamily" (italics mine). A more definite statement is in Opinion 133. This Opinion dealt with the type genus of a "family" (family name) but did not give a definite rule by which to choose between two different family names which are synonymized. These still leave the choice open, as does the recommendation of the "Copenhagen Colloquium" of which the first phrase (only) was quoted by Bradley: "The naming of units belonging to the Family-Group of categories shall be governed by priority, except that, in cases where pri-

ority is in conflict with current usage, current usage is to be maintained, wherever, in the opinion of the individual taxonomist, this would lead to greater stability and universality of nomenclature than would the strict application of priority."

This latter statement appears to favor priority of supergeneric group name rather than priority of generic name within a family, but certainly does not make itself clear about what kind of priority is meant, and gives usage a deciding vote. At any rate, a decision on family names to be effective and lasting must be accepted and put into enough use to build a large body of precedent. Otherwise it has no real force, as it can be superceded by a different recommendation from the same or some other source, as easily as the first recommendation was made.

Family names have never been subject to rigid rules of selection, and any rigid system adopted now will result in a period of turmoil. The best system would obviously be the one that would result in the least change from present usage, and be easy to apply in order to avoid mistakes and disagreements. Any system also would best be applied gradually, only as specialists deemed it necessary to choose between names, and had all necessary information, particularly when shifts in group limits or status would bring individual questions of group nomenclature to a head. Most workers seem to feel the need of some system to give consistency and force to the necessary nomenclatural decisions, but at the same time are cautious about coming to a decision on what system to use, or applying any system with thoroughness. My own view is that to name families and similar groups from the oldest included genus is the better system and my reasons are listed below. (1) The bibliographic data are at hand for this system, while data for priority of supergeneric group names are not cataloged well enough for a sound nomenclature to be built on it. (2) It avoids the question of how to deal with the infinite variations in concept and form of the group names in older literature, which would inevitably cause confusion and disagreements. (3) It avoids much confused thinking and lack of agreement resulting from false analogies with the type system used for genera and species. (4) It *appears* to be the system that will make least overall change from present usage. (5) It is a system definitely suggested in older codes of nomenclature, during the time when many of our family names were being proposed or stabilized.

The above argument does not, of course, settle the question of rules for family names. It is for a future generation to show which system, if any, is to be sanctioned by general agreement and practical application. In the meantime, there are good nomenclatural reasons to continue using the name Psammocharidae rather than shift to Aporidae.

There remains the more general question brought up in Bradley's article concerning the validity of a nomenclatural decision by an individual in opposition to a decision by a group. The petition to have *Pompilus* made a *nomen conservandum* and to suppress *Psammochares* was circulated by Bradley in 1928. To fix firmly the application of the name *Pompilus,* the petition requested that *Sphex viatica* Linnaeus be its type. The petition was signed by fifty-eight hymenopterists. This looked like good backing, but what actually did it mean? As far back as the time of De Geer and Geoffroy *Sphex viatica* was known. to be the species generally called *Podalonia hirsuta* (a sphecid). It was sometimes confused with *Sphex fusca* Linnaeus (a psammocharid), but as long ago as 1789 Villiers pointed out (*Caroli Linnaei entomologia . . . , 3*: 230) that the two species should not be confused, and listed the distinctions between them. All fifty-eight

(*Concluded on page 192*)

A Problem in Taxonomy: the Sponge Genus *Reniera*

M. W. DE LAUBENFELS †

SYSTEMATIC zoology is deeply concerned with the International Commission on Zoological Nomenclature and its rulings. Examples of procedure may be discussions of mammalian names and yet interest a spongologist; perhaps examples of nomenclatural problems in sponges may similarly interest mammalogists. The problem of names, and of the International Commission, may be well put before an audience of systematic zoologists by taking an outstanding problem in the determination of correct names for Porifera.

The generic name *Reniera* is one of the most widely used of all that pertain to animals of the phylum Porifera. Some two hundred and seventeen Recent species have been described for this genus, and various fossil forms have also been assigned to it. Many of these Recent species are common and have been used in physiological work, therefore increasing the use of the name.

A species which has been called *Reniera cinerea* exemplifies to a high degree the characteristics that have become associated with the name *Reniera*. Most emphatically it is not the type species, but it is thoroughly representative. It is widespread along the shores of at least the Atlantic and Pacific Oceans, common on both east and west coasts of North America, and is a relatively conspicuous species.

This species is a sponge that grows in an encrusting manner over stones and generally is lavender in color. It has practically no ectosome at all, no dermal specialization; the endosome merely comes to the surface and stops. The architecture is of the sort called isodictyal, which means that there is a pervasive reticulation (in this case somewhat vague) made by spicules mutually conjoined at their tips by small amounts of spongin. These spicules are siliceous, and of the simplest kind, merely smooth rods, pointed at both ends; these are termed "oxeas."

Many problems are involved in regard to the name *Reniera* and its animals. Not the least is this: it is well known and quite to be expected, that degenerative simplifications occur in the Porifera. Those sponges that have been called *Reniera* may be polyphyletic. Other sponge sorts may have gravitated to this level by loss, in one case of this and in another case of that other characteristic. That which was called *cinerea* may really represent a score or more of genuinely different species, for which mankind merely lacks the means of proper discrimination. There are, for example, many species of bird that a blind man could not tell apart. Equally perplexing is the exact opposite; many sponge species of this general sort are set off from one another by only such small differences as average spicule size; many of these perhaps should be dropped into synonymy.

The nomenclature of this kind of sponge is another vexatious problem, one that has caused much confusion, yet possibly one that could be solved or resolved. An historical approach may prove useful.

An Italian named G. D. Nardo started the puzzle in 1833. In that year he was the author of an article in a journal, the *Isis,* which did not number it pages. In its column number 519 Nardo set up the genus name *Rayneria.* He described it as follows:

"Aggregata polymorpha magis aut minus porosa et foraminosa, tenacitate fere nulla, facile digitis pulverizabilia in sicco. Fulcimente aculeiformia inconspicua

† Professor de Laubenfels died on February 4, 1958, at Corvallis, Oregon, while this paper was in press.

simplicia, dispositione vario materiei animalis ope conjuncta ut pulpam uniformem praebat."

Many sponges answer to this description and Nardo did not describe any species. Worse yet, no one has ever yet described any species of *Rayneria,* thus it stands as a "sacred" genus, a very real menace to nearly every sponge genus erected since 1833; i.e., to about 99 percent of all genera of Porifera.

A most distressing and serious situation stems from one of the most amazing decisions that has been rendered by the International Commission on Zoological Nomenclature. Presumably they did not forsee such situations as this one, but they should have. In their Opinion 46 the members of the Commission ruled as follows:

"If it is not evident from the original publication of the genus how many or what species are involved, the first species published in connection with the genus becomes *ipso facto* the type."

In 1833 only a score of sponge genera had been established; about 1,500 have been established subsequent to that date. Today one can look over the many and pick out one of them that is a much used generic name. He may then announce that he chooses the type species of this genus to receive the sleeping name *Rayneria,* and it will *ipso facto* become *Rayneria,* and the more recent genus will maddeningly fall in synonymy.

A comparable systematic procedure can be used to solve the problem, and is therefore here essayed. The *"ipso facto"* type of *Rayneria* may be selected from one of the few genera that were established before 1833. One of these is the genus *Halichondria,* of which the type species is the species *panicea.* (First described as *Spongia panicea* by Pallas in 1766, page 388, and used as type for his new genus *Halichondria* by Fleming in 1828, page 520.) This species, *panicea,* fits beautifully the generic diagnosis given by Nardo. It is here and now set definitely as the type species of *Rayneria* according to Opinion 46 of the International Commission. *Rayneria* and *Halichondria* thus become congeneric, having identical type species, but the 1833 name falls as junior synonym to the 1828 name.

Now we come to the name *Reniera.* The same G. D. Nardo in 1847 was the author of an article entitled "Prospetto della fauna volgare del veneto estuario" (Prospectus of the common fauna of the estuary of Venice). In this, on page —,* he uses the word *Reniera,* its first appearance in print. Nowhere does he say that this is the same as his 1833 *Rayneria,* but it fills the same nomenclatural niche that his *Rayneria* filled. Neave in his "Nomenclator Zoologicus" says of it "(? pro *Rayneria* Nardo 1833)." If it is merely a new spelling or mispelling of the earlier name, then, in that case, it automatically falls in synonymy to the earlier name, as Nardo's 1847 *Hircinia* falls to his 1833 *Ircinia.* Not even the original author has the right to change the spelling of a name, once it is published. Yet does *Reniera* equal *Rayneria?* This is not at all certain, although probable. One must envision the possibility that *Reniera* is a wholly new genus in 1847.

Nardo gave species to his *Reniera,* and (perhaps for that reason) subsequent zoologists have taken up the name. Zoologists in general do not have a high regard for genera that are nothing at all but black marks on white paper, although Opinion 46 sets supreme value on such. Nardo described *Reniera* thus:

Ne medesmi luoghi e sulle pietre delle rive di approde e dei palazzi vedesi sempre piú o meno sviluppata, nella fredda e temperata stagione, la nostra Reniera flava, a cui meno copiosa é commista la Reniera forcellata N. Il tipo del genere, o Reniera typica, che termina per lo piu in ammassi tubulari, s' in contra pure frequente, e lo stesso é da dirsi di altre due specie distinte col nome di Reniera variabilis e di Reniera atra.

* This page number was to have been inserted by Professor de Laubenfels into the proof. It has not been possible to ascertain the page to which he referred. *Ed.*

This can be translated:

In both the cold and temperate seasons our Reniera flava, which is mixed with Reniera forcellata N. though the latter occurs less abundantly, can always be seen more or less well developed in these same places on the landing stones of the river banks and of the palatial houses. The type of the genus, or Reniera typica, which terminates in great tubular masses, is encountered rather frequently, and the same can be said of two other distinct species, having the names Reniera variabilis and Reniera atra.

The type species is the only one that absolutely belongs to the genus. Occasions have arisen in which, rather than take the type out of a large genus, every other species was instead removed (and properly). Thus all that is certainly known about *Reniera* is that it included the species *typica* and the characteristics of this *typica* must be those of the genus.

Thus *Reniera* is fixed upon a type species of which no specimens exist, and about which all that is known is that "it terminates in great tubular masses." This is true of vast numbers of sponge species, especially those that grow in water of little current. It has been appropriately suggested that the elevation of the oscule (exhalant) reduces the danger that newly ejected water might be at once sucked back into the pores (inhalant).

Sponges of the genus *Halichondria* commonly have masses of tubular projections (oscular chimneys) over their surface. It is therefore here suggested that Nardo's *Reniera typica* was an *Halichondria,* and that the name *Reniera* be dropped in synonymy to *Halichondria* for this reason, if for no other. One might select some European specimen of *Halichondria,* perhaps in the British Museum of Natural History, and designate it as lectotype of *Reniera typica.*

The multitude of sponges that have been identified as *Reniera* still need to be considered. What is, or what are, their names? In an effort to clarify this, one may go back to "Dead man's fingers." Two of the sponges that have been noticed by non-specialists for centuries are the two that are so common on the shores of Europe and North America, and known colloquially as the "Bread sponge" (*Halichondria panicea*) and "Dead man's fingers." The latter is purveyed by biological supply houses under the name of *Chalina,* in fact it has been so designated for a long time, quite erroneously.

Linnaeus noticed few sponges, but the famous "finger" sponge was one of the few that he did name; he called it *Spongia oculata* [he put all sponges in the one genus, *Spongia* (1759, p. 1348)]. About 57 years later zoologists began realizing that additional genera were necessary, and one of the earliest to obtain such recognition was *oculata.* In 1841, page 5, Robert Grant made it the type of his new genus *Haliclona.*

In 1861 Grant published a tabulation of names, one of which (page 76) was *Chalina.* It was a *nomen nudum,* without description or species. In 1862 (page 1120) J. S. Bowerbank discussed *oculata,* and stated that it was type of Grant's genus *Chalina,* but because Grant's *Chalina* was a *nomen nudum,* by the rules this name takes its beginning from Bowerbank's use thereof. Because *oculata* is the type of both the earlier *Haliclona* and the later *Chalina,* they are synonyms, and the later falls as junior to the earlier name. Unfortunately very many authors have used *Chalina,* following Bowerbank; for example, a sterol, discovered new in *Haliclona,* has been named chalinasterol.

It was soon noticed that the internal structure of *oculata* was much like that of sponges of the *Reniera cinerea* type, and recent authors, especially Burton and de Laubenfels, have therefore treated all such species as belonging in the genus *Haliclona.*

Merely to drop *Reniera* in synonymy to *Haliclona* can be criticized because of the great difference in form involved. It can be defended in view of the fact that the bush-like "Chalina" type, as a juvenile, passes through an encrusting or "Reniera" stage. It is certain that many

encrusting *Haliclona* would have gone on to become ramose had they not been collected. Other species of *Haliclona* remain encrusting regardless of age and environment. The points of agreement are so great that only one genus may be required, but to allow for a "sorting out" process, de Laubenfels (1954, p. 64) established the subgenus *Reniclona* for those *Haliclona* that answer to the description which has been associated with the name "Reniera."

Now what of our *Reniera cinerea*? Grant named it (1825, p. 204) as *Spongia cinerea*. Burton (1934, p. 535) felt the need of a specimen for this name, and picked out one from the British Museum of Natural History as a neotype; he was sure that this represented what Grant had in mind. Yet this neotype is of the genus *Adocia*, which has a distinct ectosome, absent from *Haliclona*. The name thus becomes *Adocia cinera*. This is also a fairly common sponge, but it leaves a problem for the commoner ones that had been being called *cinerea*.

In 1866 Bowerbank brought out the second volume of his *Monograph of the British Spongiadae*, to which reference has already been made. In this volume he describes many species of his genus *Isodictya*. Burton wrote about them in 1926, making it clear that many of them were and are synonyms of that which at that time was still called *Reniera cinerea*. These specific names are the oldest ones available for the necessary renaming of this *cinerea*-concept. In 1936, page 40, de Laubenfels looked them over and selected *permollis* as most suitable for this purpose.

Therefore, we may summarize those remarks by the following lines:

1. *Rayneria* is a junior synonym of *Halichondria*.

2. *Reniera* is a junior synonym of *Halichondria*.

3. Most sponges identified as *Reniera* are *Haliclona* (*Reniclona*).

4. Sponges identified as *Reniera cinerea* are *Haliclona permollis*.

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M. W. DE LAUBENFELS until his untimely death had been a teacher and investigator for a third of a century. He had received his training at Oberlin and Stanford University, and had taught at Pasadena City College, the University of Hawaii, and Oregon State College. Dr. de Laubenfels' studies of the Porifera are unparalleled in American zoology: he published forty papers, several of which are monographic in scope. At least four of his papers were in press at the time of his death. Besides his work on the sponges, Dr. de Laubenfels published on bird distribution and taxonomy, navigation by Central Pacific natives, an hypothesis on dinosaur extinction. In addition he was the author of a successful general biology text.

Some Bases for Higher Categories in Classification

CHARLES D. MICHENER

THE purpose of this paper is to discuss, and I hope clarify, some issues relating to the functions and uses of genera and other higher categories. It has been quite natural to use as a basis of discussion a previous paper (Michener and Sokal, 1957) on a statistical approach to problems in classification, but the greater part of the present paper has significance with or without a quantitative background of this sort.

The paper has been written with categories such as genera or families in mind; some of its contents would be applicable in only a general way to very high categories such as classes and phyla. Sometimes, to provide for simpler expression, the word genus is used to imply also other similar categories.

Types of Classifications

Hierarchies of categories such as genera might be established for convenience alone, using arbitrarily selected characters. In that case the classification would serve only as a method of organizing information. Probably size of the units (e.g. number of species in a genus) would be a main factor in determining whether or not they were convenient. Enormous units are inconvenient, and numerous monotypic units are neither useful nor informative. Few biologists would advocate a wholly arbitrary classification such as this.

In contrast to classifications of convenience are natural classifications. This expression is often taken to mean classifications based on phylogenetic relationships. However, pre-Darwinian authors discussed natural classifications and obviously meant classifications based on numerous characters, and the term is used in the same sense by modern authors (e.g., Mayr, Linsley, and Usinger, 1953). Natural classifications as used today attempt to portray either (1) degree of difference (or similarity) among forms, i.e. the amount of evolution that separates the forms (from which we deduce evolutionary progress), or (2) levels of connections of the branches of a phylogeny. Natural classifications today are concerned with the "what?", "why?", and "how?" of evolution. Most classificatory attempts by systematists are compromises between classifications of convenience and classifications that are as natural as possible. Much of the rest of this paper consists of a discussion of the properties of two sorts of natural classifications, the possibilities of coordinating or equating them, and the possibilities and desirability of modifying them by considerations of convenience.

Natural systems may not be compatible among one another. They are based on relationships, but we usually neglect to specify what kind of relationships we mean. One sort of natural system is based on static or absolute relationships, i.e., on the differences (or their complements, resemblances) that actually exist among groups, without reference to probable or known phylogeny. The other sort of natural system is based on assumed or known phyletic relationships. As will be shown below, these two types of natural classifications, based on different kinds of relationships, cannot be portrayed by the same tree of relationships nor can their main features be shown by the same hierarchy of categories (genera, tribes, subfamilies, etc.).

Static Relationships

Concrete data on static relationships are usually lacking because authors rarely give any real measure of resemblances for more than a few characters. A recent paper (Michener and Sokal, 1957) provides such data, however, for many characters in a group of megachilid bees called the *Hoplitis* complex. This paper suggests one scheme for dealing statistically with very numerous characters among a large group of species; 96 species were treated. For details of the method, called the weighted variable group method, see Sokal and Michener, 1957. The method is based on correlation coefficients among the species, computed from data on the 122 known characters. By grouping the species with highest correlations, small groups were developed. Then with new correlation coefficients based on the groups as well as on isolated species that had failed to enter the small groups, larger groups were established. The process was continued, and the resulting hierarchy could be represented by a tree-like diagram of relationships.[1]

Such diagrams represent relationships in a static, non-historical, or absolute sense. The amount of evolution (evolutionary rate times time) separating any two species in the study can be judged by the level at which the lines representing the species are connected. Since the levels of the forks of the diagram are determined objectively, they may be compared with one another and used in the classificatory process in a way that would not be justifiable in ordinary subjectively prepared diagrams of relationships. One can draw horizontal lines across our diagrams of relationships (Fig. 1, also figures 5 to 8 of Michener and Sokal, 1957) at arbitrarily chosen levels. One such line might, for example, represent the genus level and one would recognize as many genera as there are lines of the diagram crossing that horizontal line. This method provides a realistic description of the static relationships by means of categories; within a moderate sized group like the *Hoplitis* complex, genera of equivalent value from the standpoint of absolute relationships can be recognized.

A logical view is that these objective standards should by themselves be applied to recognition and delimitation of genera and other categories. Phyletic relationships are impossible to ascertain with certainty in most cases, and convenience can be considered a secondary matter. Moreover, static relationships are a measure of the amount of evolution that has occurred between the various forms studied, and as such are biologically of as much interest as phyletic relationships. The only simple method that we know of that can approximate a realistic description of relationships is a pictorial one (treelike diagrams); it can diagram either static relationships or phyletic relationships. Genera or other categories developed from such diagrams are therefore ambiguous if one tries to satisfy both types of relationships. My colleague, Dr. Robert R. Sokal, maintains, for example, that it is illogical to classify *Proteriades*, which connects to *Hoplitis* at a high level (Fig. 3), as a genus, while at the same time regarding *Dasyosmia*, connected to the rest of *Hoplitis* at a much lower level, as a subgenus of *Hoplitis*. (Reasons for this arrangement will be discussed later.) Rather than use categories in this ambiguous manner, he would prefer to utilize them to show static relationships only, leaving the description of descent, i.e., phyletic relationships, to separate diagrams. Such a course in the *Hoplitis* complex would have led to recognition of several more monotypic subgenera as well as more very large subgenera, had the total number of subgenera remained near the presently accepted number.

It should not be inferred that static relationships have been obtained and used only in such rather ambitious quantita-

[1] Remarkably similar methods were independently developed by Sneath (1957*a*, *b*).

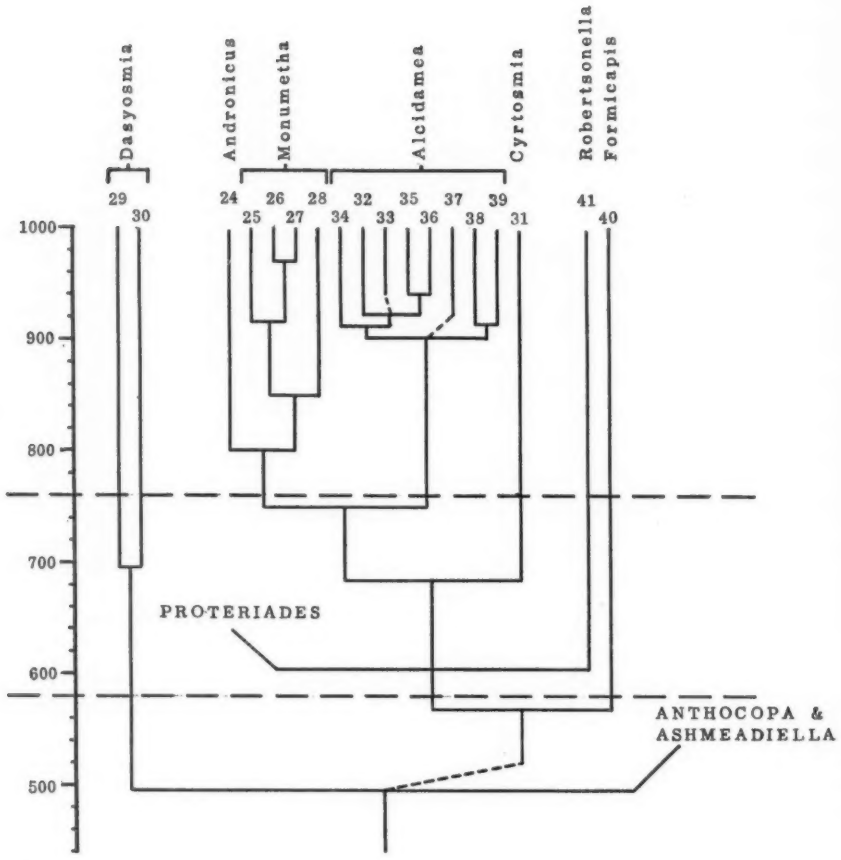

FIG. 1. Diagram of static relationships for the American subgenera of *Hoplitis* obtained by the weighted variable group method (after Michener and Sokal, 1957).

The ordinate indicates the magnitude of the correlation coefficient multiplied by one thousand. Correlations between any two joining stems can be found by reading the value on the ordinate at the level of the horizontal line connecting the stems. Broken lines where more than two lines join are for convenience only; the horizontal connecting line has the same significance as elsewhere. This method was used to avoid any suggestion that position of a stem to the right or to the left has significance. Figures at the tips of the lines represent numbers of species. Subgeneric names are indicated in vertical positions above them. Names of allied genera are indicated horizontally near the bottom of the diagram. Horizontal broken lines indicate ways in which the diagram can be used in the recognition of genera, subgenera, etc. that are relatively comparable in degree of difference from one another.

tive studies as that described above. Comparative serological data are regularly presented as quantified static relationships. Moreover, subjective estimates of static relationships are used by all taxonomists interested in relationships. The conflict between static and phyletic relationships is evident, for example, whenever a taxonomist discusses some striking form and says that in spite of its remarkable (static) characters, it is closely related (phylogenetically) to ————.

Further, it should not be inferred that static relationships necessarily are studied without weighting of characters. Taxonomists often weight characters and then study static relationships, that is, they consider differences in certain characters more important than differences in others. Presumably, this is the method advocated by Borgmeier (1957). It is obvious that if one studies but few characters, weighting is necessary to produce a satisfactory classification whether it is based on static or phyletic relationships or on a combination of the two. It is only when one studies many characters that it is possible to increase the objectivity of the classification by omitting any subjective weighting of characters. If the number of characters studied is large enough to provide a representative and random sample of all the characters, and thus of the genetic differences among the organisms classified, weighting becomes unnecessary and indeed objectionable because of its subjectivity.

Phyletic Relationships

When systematists speak of relationships, they think primarily of phyletic ones, with a certain, often unrecognized, component of static relationships entering their thinking. Earlier classifications of the *Hoplitis* complex had been based largely on ideas of phyletic relationships obtained from studies of characters and consideration of ecological adaptations, etc. When the diagrams of static relationships prepared by the weighted variable group method (figures 5–8, Michener and Sokal, 1957) were compared with diagrams of presumed phyletic relationships (figures 1, 2, Michener and Sokal, 1957), one type of difference appeared several times. Various distinctive species or small groups were shown by the statistical method to be much more isolated than by classical methods of systematists. This brought up what we called the pregroup-exgroup problem, graphically illustrated by diagrams of phyletic relationships in Figure 2. The correlation coefficient between species x and the other members of the group might be equally small for relationships such as are depicted in A and B of figure 2, so that by the weighted variable group method, similar diagrams of relationships (more like A) would result. Yet the phylogeny would be very different in the two cases. Whether this would influence treatment at the generic level will be discussed below.

The problem could, of course have been "solved" by appropriate subjective weighting of characters. However, a scheme was ultimately developed (Michener and Sokal, 1957) for objectively correcting for the pregroup-exgroup prob-

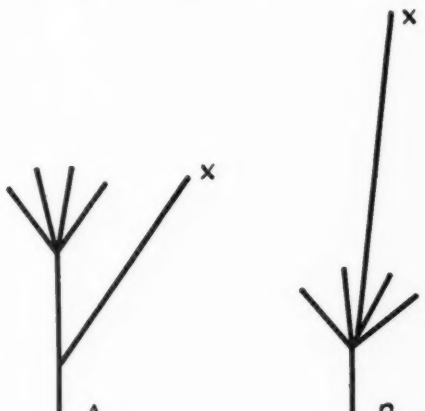

FIG. 2. Diagrams of hypothetical phyletic relationships to illustrate the difference between pregroup (*A*) and exgroup (*B*) species, marked x in each case.

lem to produce modified diagrams of relationships [2] which more nearly resemble phylogenies than the initial diagrams. Figure 3 is such a modified diagram; the exgroup lines which in the original diagrams (Fig. 1) were connected at much lower levels are marked by black spots.

It should be clear that diagrams of relationships such as Figure 3, while objective in the sense that they were devised by following a predetermined technique in their construction, may be rather different from true phylogenies, which, of course, cannot be determined. Perhaps they come as close to resembling phylogenies as anything that we can prepare with available data. However, some of the possible shortcomings have a bearing on the problems of genera. One such shortcoming is that since the technique dealt with relationships, it ignored the sizes of gaps between genera. The importance of this factor will be considered under a separate heading below. Of course extinctions, exclusion of certain species because of insufficient data, etc., would also influence the diagrams in at least minor details. For purposes of the discussion in the remainder of this paper, however, Figure 3 will be taken to be phylogenetically accurate, even though we know that, without an extensive fossil record, real phylogenetic accuracy is unattainable or at least cannot be proved.

It will perhaps be useful to remark here that while the morphological or static relations among a group of forms can only be properly represented by multidimensional methods, the phyletic relationships can be shown in two dimensions, as in Figure 3. If one imagines a complete phylogenetic tree of a group, there is nothing in it that cannot be shown in two dimensions. It is only when one tries to add more information, such as degree of morphological divergence, that slopes or lengths of branches or distances between branches (according to the convention) become important and impossible to reconcile with one another in two- or three-dimensional space. In discussions of dendrograms and their construction, confusion between phyletic and static relationships pervades much of the literature.

As shown above, the present system of naming categories cannot always show both phyletic and static relationships. Thus, referring to Figure 2, it will be found difficult to devise a single nomenclature to differentiate situations *A* and *B*. If we call both *A* and *B* genera, for example, we reveal nothing of the different origin of *X* in the two diagrams. On the other hand, calling *X* a separate genus from the cluster of species in *A* but including *X* in the same genus as the cluster in *B* implies that *X* is closer to the cluster in *B* than in *A*. This is true from the standpoint of time of divergence (phylogeny), but not from that of amount of evolutionary change (static relationships). Since most zoological systematists give greater weight to phyletic than to static relationships in devising classifications, the latter course would probably be taken by many workers. It was taken in preparing Figure 3 where some exgroup species do not appear (they were considered to be included in various subgenera) while the others are given only subgeneric status, although on the basis of static relationship (or its corollary, degree of difference) each of them might well have received generic or subgeneric status (see Figure 1).

Perhaps, the reason that most systematists place great weight on probable phyletic relationships in delimiting genera is

[2] Further modification of the original diagrams of static relationships might have resulted in more accurate diagrams of descent (phylogeny). If the exgroup species and groups were eliminated after the first analysis and then a new weighted variable group analysis performed, the connections ought to be more accurate phylogenetically. As matters stand now, exgroup species strongly influence connection of major groups with one another. This is illogical, since the exgroup species concerned arose after the phyletic divergences represented by the connections.

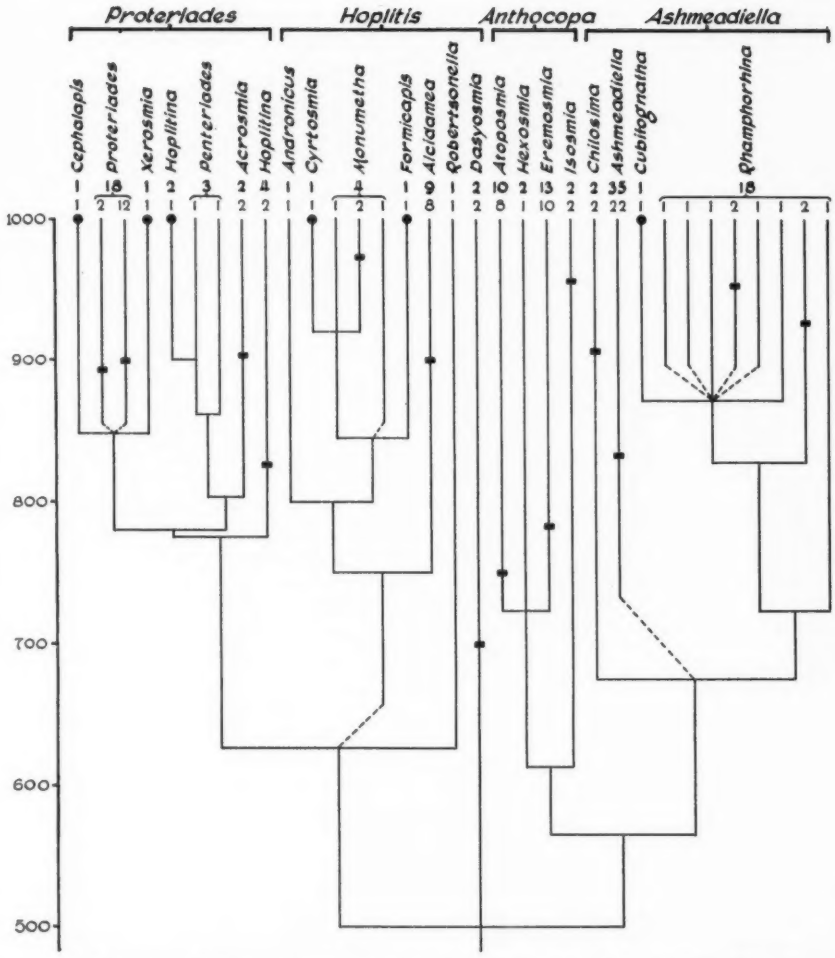

FIG. 3. Summary diagram of assumed phyletic relationships within the *Hoplitis* complex (prepared from figures 12 to 15 in Michener and Sokal, 1957). Exgroup subgenera are indicated by a spot at the summit of the line. Except for these subgenera, the ordinate has the same significance as in Figure 1, as do the broken connecting lines. Bars across lines indicate the lowest levels at which the various stems divide into species which are not shown separately. The number of species represented by each line is indicated by the lower row of figures above the tips of the lines. It was often necessary to show some of the relationships among species of certain subgenera, in order to indicate properly the supposed origins of the exgroup subgenera. Brackets above the lower row of figures associate the lines separated for this purpose. The upper row of figures indicates probable total numbers of species in each subgenus, including certain forms not included in the original study and hence excluded from the lower row of figures. The subgeneric names are vertical, and are associated by brackets into the four genera, whose names are written horizontally.

that a genus, although undefinable as to the size of the phyletic branch that it encompasses, is almost unanimously regarded as a unit that should be monophyletic. Moreover, zoologists by tradition think in phylogenetic terms. Classifications based on static relationships can, of course, be made up of monophyletic units. However, these units may be quite different from those based on phyletic relationships. It is not clear to me whether or not it would be desirable to change from the traditional approaches emphasizing phylogeny to approaches utilizing only static relationships. The main disadvantage of the phylogenetic basis for classification is that the data for ascertaining true phylogenies on which to base classifications are usually not available. This seems exceedingly serious until one realizes that data for weighted variable group analysis of static relationships are also not generally available. Such data can be obtained, however, in the course of any revisional study, while data for true phylogenies will probably never be obtained for most groups.

Gaps

Morphological gaps in a sequence of species are probably of secondary importance in deciding generic limits. This is especially true in any study which, like the weighted variable group method, uses quantitative estimates of static relationships, because the gaps are major factors in determining how the species will be grouped in the first place. Obviously, correlation coefficients will be relatively low among species on different sides of a gap, so that groups of species on each side of the gap will fall together on the basis of static relationships in the weighted variable group method.

At the generic level gaps are perhaps more easily appreciated than proximity unless one gathers extensive data for the study of the latter, as was done in the case of the *Hoplitis* complex. Perhaps for this reason attention has been given to gaps in connection with the generic problem in the past. For example, Mayr, Linsley and Usinger (1953, p. 48) say, "A genus is a systematic category including one species or a group of species of presumably common phylogenetic origin, which is separated from other similar units by a decided gap. It is suggested for practical reasons that the size of the gap be in inverse ratio to the size of the unit. The latter qualification will prevent the recognition of unjustified monotypic genera."

It is a matter of practical fact that every species has to go in one genus or another. Species that might almost as well be placed in one genus as another are a problem to any taxonomic work. (They are often interpreted to indicate that two genera should be joined.) The weighted variable group method at least indicates what genus they most logically enter. The method itself has a tendency to exaggerate the apparent importance of such gaps as exist. An example will illustrate this point: Consider two species, 1 in genus *A*, 2 in genus *B*, the species rather similar to one another, yet each more similar to other species in its own genus. The other species of *A* are more different from *B* than is 1, and the other species of *B* are more different from *A* than is 2. Figure 4 is a diagram of phylogenetic relationships which might result in such a situation. The gap between the genera will be in fact rather small because of the similarity of 1 and 2. By the weighted variable group method, species 1 is first placed with other species in its genus and 2 with other species in its genus. Only later, when the closeness of 1 and 2 is obscured by averaging with other species in their respective genera, is the correlation (level of the connection) between the genera ultimately obtained. The method was designed to function in this way in order to place every species in one genus or another. In practice, we found good agreement between the weighted variable group method and

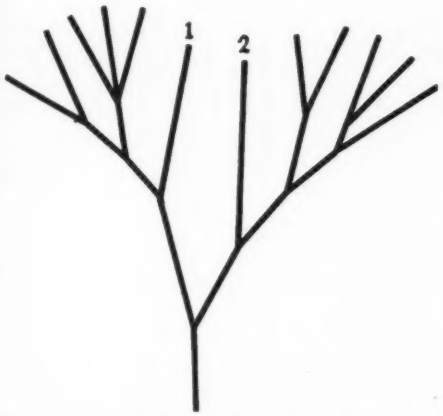

FIG. 4. Diagram of hypothetical phyletic relationships. For explanation, see text.

previous ordinary systematic approaches, when consideration was given to the fact that the latter are based on the investigator's best judgement of phyletic relationships while the former merely attempted to show non-historical or static relationships.

Since vertical distance in weighted variable group diagrams indicates degree of relationship, gap size will usually be shown by vertical stems which will be longer, the larger the gap. There exist situations, however, in which this might not be the case. It is possible to imagine a large gap between two relatively compact groups connecting at a certain level, and a negligible gap between two other more diffuse groups which would connect at the same level because of similar average correlations between the groups. Thus gap size might vary somewhat independently of the static relationships which are determined for the *Hoplitis* complex and also independently of the more nearly phyletic relations which we determined by modifying the weighted variable group method. We plan to investigate gap sizes (measured by maximum correlation coefficients between species in different groups) with the data on the *Hoplitis* complex. We believe from initial study that the gap sizes will be correlated very highly with the static relationships of the groups, but that there will be some cases where added information will be obtained from the gap sizes.

Phylogenetically, a gap may be quite an artificial or happenstance matter, resulting from vagaries of extinction or even of collecting. In systematic work of the usual sort, where the concern for phylogeny is great, careful attention should be given to gap size. We believe that if we had all the forms that have ever lived, there would be no gaps. This ideal is never achieved even by paleontologists, but greater confusion from the standpoint of hierarchic divisions like genera arises, the nearer they approach it. Unhappily there is no assurance that it is the oldest types in an array of forms that have become extinct. Since gaps may occur anywhere, one genus may consist of representatives of two (or more) phyletic lines connected by surviving annectant forms, while another genus might belong to one of the lines, as suggested by Figure 5 A. Probably nothing short of an extensive series of fossils is likely to detect this sort of thing. Figure 5 B shows the type of diagram of relationships (phyletic or static) that would probably result from applying usual methods or the weighted variable group method to a phylogeny such as is shown in Figure 5 A. If species x and y had not become extinct, the situation would have been similar to Figure 4, and the weighted variable group diagram would have been much like the phylogenetic diagram.

Ideally, one might think that a genus should consist of a monophyletic group of species all of which are more closely related phylogenetically to one another than any one of them is to any other species outside the genus. In practice, this ideal is commonly not achieved in groups of closely related genera. For example, in Figure 5 A, species e might be more closely related to d than to n, yet for various reasons e would be congeneric

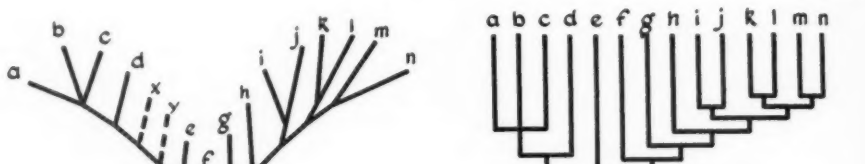

FIG. 5. *A*, Diagram of hypothetical phyletic relationships, in which species *x* and *y* are extinct. *B*, Hypothetical diagram of static relationships (e.g., one that might have been prepared by weighted variable group method) based on surviving species in *A*. For explanation, see text.

with *n* and *d* might be placed in another genus. Here is a case where, even though the phylogeny were known as shown in Figure 5 A, the main phylogenetic dichotomy might well be ignored in delimiting the genera.

Other examples, based on actual organisms, are shown in Figure 3. For example, relationships (probably phyletic as well as static) in the subgenus *Rhamphorhina*[3] had to be shown in some detail because from an advanced species cluster springs a line (if the phylogeny has been properly interpreted) leading to a single species so very divergent that it has been unhesitatingly put in a separate subgenus *Cubitognatha*. This exgroup species is separated by a striking gap from *Rhamphorhina*. By our statistical method of studying static relationships, *Cubitognatha* was also found to be distinctive. Thus, as is commonly the case, the status indicated by studies of relationships and by consideration of gaps was the same.

This need not always be the case. A familiar example at a higher level concerns the beetle families Chrysomelidae and Cerambycidae. I think that relationships based on central tendencies, such as we used in preparing Figure 3, place these families well apart. Yet there exist a few genera scattered between the families and almost completely linking them, so that the gap between the families is almost nonexistent. The families might well be united except that each is very large, a good example of the importance of group size in determining our usual taxonomic practice.

Group Size

According to the method of static relationships, the number of species included in a group is of no concern in determining the rank in the hierarchy to which the group will be assigned. Neither enormous genera nor monotypic genera are to be avoided by this relatively objective method. The number of species in a group has often been important in deciding the level in the classificatory hierarchy to which the group should be assigned. The importance of group size in usual systematic procedure is easily appreciated in connection with high categories. *Archaeopteryx* would be regarded as a peculiar feathered reptile, had not the large group of birds evolved. Or to turn to neozoology, if there were but one

[3] Mr. K. V. Krombein has pointed out to me that the proper name for this group is *Arogochila*.

genus of pollen-collecting sphecoid wasps, they would be considered as just that. It is only because there are hundreds of genera and thousands of species that the bees are customarily placed in a superfamily separate from that of the sphecoid wasps.

The same principles apply to genera, and have influenced the decisions as to categories recognized in Figure 3. Thus *Proteriades* is accorded generic rank even though it branches from *Hoplitis* at a rather high level. This is because of its rather numerous species (23 in the statistical study, 31 in total, perhaps). Most of these species are morphologically adapted to collect pollen from flowers of *Cryptantha*. The success of the group is probably a result of the adaptation to this plant, whose pollen is inaccessible to most other bees. If there were but one species adapted to *Cryptantha*, it would certainly be placed in the genus *Hoplitis*. *Proteriades*, as now understood, contains a few primitive species which are not adapted to *Cryptantha*. Some of them are probably similar to the ancestral species in which adaptations to *Cryptantha* first appeared; these adaptations ultimately permitted much speciation and were therefore responsible for the generic rank now given to the group.

The converse of the *Proteriades* situation is exemplified in Figure 3 by *Dasyosmia*, a very distinctive group called a subgenus of *Hoplitis*. It contains only two species, themselves almost as different from one another (as shown by the correlation coefficients) as is *Proteriades* from some sections of *Hoplitis*. Yet for the sake of convenience, and to avoid excessive multiplication of names, the two species are left together in one subgenus and assigned to the genus *Hoplitis*. Inclusion of these forms in *Hoplitis* means (see Fig. 3) that *Proteriades* arose from forms that would be called *Hoplitis* if they existed today, i.e., it is a sort of offshoot from *Hoplitis*.

Similar situations at the subgeneric[4] level can be seen elsewhere in Figure 3. *Cephalapis* and *Xerosmia* arose from forms that, were they living, would be included in *Proteriades* s. str., *Cyrtosmia* and *Formicapis* arose from *Monumetha*, and *Cubitognatha* from *Rhamphorhina*. All these derived subgenera were based on exgroup species. Because of their distant static relationships to their nearest relatives and the large gaps which, therefore, isolate them, they were regarded as distinct subgenera, in spite of the fact that each contains only a single species. Indeed two of these monotypic subgenera were long ago accorded generic rank, as were several of the other subgenera shown in Figure 3, and have only rather recently been reduced to subgeneric levels.

These examples suggest a matter which seems to me basic to construction of a good classification. Other things being equal, it is probably better to recognize genera that represent major phyletic lines rather than mere terminal branches. Phylogenetically this can be illustrated by Figure 6. It would probably be more meaningful to divide this hypothetical group by the broken line into two genera than to recognize three monotypic specialized exgroup genera, *a*, *b*, and *c*, with all the other species remaining together. The latter treatment is, however, very common. It might be supported by weighted variable group analysis, in which *a*, *b*, and *c*, would probably join the main stem quite low in the diagram. Generic status for *a*, *b*, and *c* is especially to be deplored because after *a*, *b*, and *c* have been removed, other distinctive species can usually be found which can also

[4] I recognize the validity of arguments against the use of subgenera (e.g., they are simply additional names representing the indecision of the author; species groups, sections, etc., would do equally well without cluttering the nomenclature with formal names). I continue to use subgenera because the practice is well established in the bees and because I find it convenient.

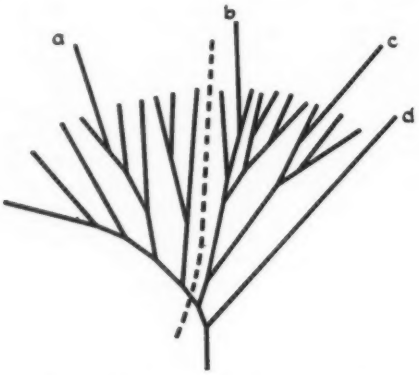

FIG. 6. Diagram of hypothetical phyletic relationships. For explanation, see text.

be given names. The process may proceed until most of the species have different generic names. In the absence of something comparable to weighted variable group analysis, nothing but the judgement of the investigator can give us an idea as to whether such isolated species are so different from their relatives that they require generic segregation. In case of doubt, it should not be accorded them. I have been more willing to accord generic distinction to an isolated pregroup species (e.g., *d*, Fig. 6). It must be noted, however, that it is often very difficult in ordinary taxonomic studies to determine the position of a broken line such as is shown in Figure 6 or to define the resulting genera. Sometimes separation of forms such as *a*, *b*, and *c* is desirable for practical reasons, to make functional keys and descriptions possible for the remaining genus or genera.

In practice, a major function of a genus is to provide a convenient collective term for the included species. In this connection, the number of included species is a prime factor. It is useful and informative for non-taxonomists as well as taxonomists to be able to say, for example, that the species of *Andrena* hibernate as adults in the soil or that those of *Culex* lay eggs in rafts. It is no less useful, especially for taxonomists, to be able to make morphological generalizations about equally large groups. The tendency to break up genera for no good reason is to be deplored, although of course it is obvious that for the sake of making genera within a family more or less coordinate throughout the world, or to eliminate polyphyletic or otherwise unsatisfactory genera, divisions often have to be proposed.

Nature of the Genus

When we associate species in a genus, we are uniting together under a common heading species, all of which are different, but which seem to us to have certain phyletic and static relationships to one another. The genus contains the characters of all of its members. It has averages with regard to the characters of its various species, but as Simpson (1953, p. 341) says, "it has no single, crystallized, idealized pattern or morphotype."

It is quite true that the high categories such as orders and classes and especially phyla are sometimes recognized only as phyletic units or evolutionary branches. Often the members of such a branch are sufficiently diverse that the branch cannot be easily defined. There may be no diagnostic characters common to all the species. Think of trying to write a definition of the Crustacea or Arthropoda in such a way as to include adult *Sacculina* or of the Insecta in such a way as to include female *Stylops*, to mention extreme examples. These examples are in a sense inconclusive, since with consideration of the immature stages, these organisms can be placed in their proper groups by means of diagnostic characters. This need not always be the case, however.

With families and genera, it is much more usual to find the included species sufficiently similar that the units are clearly definable. Indeed the practicing taxonomist, faced with problems such as

making workable keys and descriptions, usually recognizes a genus by characters common to all the included species. This may tend to lead to a typological philosophy, in which one compares species with a *preconceived* idealized pattern of a genus to decide whether or not they are to be included. This is undesirable; the genus is not *defined* by characters, in the sense that one decides on the decisive characters and thereafter any species that do not exhibit the proper characters belong to other genera. On the contrary, the genus is to be recognized by similarities in the *total spectrum* of characters among the species; that is, as explained by Sneath (1957*a*), it is a group of species with many features in common but not necessarily always possessing any particular feature. Fortunately, genera usually do have certain distinctive characters common to all the species, making them readily definable units.

Since, in so far as knowledge can guide us, a genus should be a monophyletic unit, the common characters which its species possess will often have descended from the single common ancestor which broke up to form the genus. Although evolutionary rates vary, it follows in a general way that the species of a category such as genus have more common characters, having more recently diverged from their common ancestor, than do the species of the higher category (e.g., family) of which the genus is a part.

Michener and Sokal (1957) remark that in the process of a study of relationships, the working systematist normally tries to use as many characters as he can find, but is hampered in his study of character correlations by the limitations of the human mind. Also, he is necessarily subjective in the choice and weighting of characters.

If he notes that certain characters vary erratically with respect to one another among various species, the systematist will regard the numerous combinations of such characters as valuable in differentiating species, but will not use these characters in erecting higher categories, such as genera. On the other hand, when he finds several characters which are not related by function or other obvious causal mechanisms, consistently associated with one another among several species, and a quite different combination of characters associated in another group of species, he feels that he has found evidence of two species-clusters and probably of two phyletic lines (perhaps genera). The more numerous are the differentiating characters associated within each group, the more confident is he of the conclusion. Even though they may be minute and inconspicuous, the systematist will weight such characters heavily in comparison with those which vary from species to species with no obvious relation to one another. His judgements as to relationships, and hence higher categories, will therefore be largely based upon a few characters which he finds to be perfectly associated. Such a procedure is likely to lead to the situation mentioned previously, in which in practice if not in philosophy, the genus is defined in the systematist's mind by certain characters and thereafter species not exhibiting those characters belong, by definition, to other genera.

This practice is less likely if one considers why the blocks of common characters distinctive of a genus should be associated in all the species. Common ancestory is an incomplete answer. The characters presumably remain associated because, taken together, the characters have adaptive values higher than that of the various characters separated from one another. In this context, a change of one character of a block of associated ones could merely mean adaptation of a species to some different environmental feature, rather than a difference so fundamental as to suggest generic segregation.

It is evident from the above remarks that a category such as genus, as it is ordinarily used, can only be defined as

a monophyletic unit of one or more species, differing in some ways from other such units.

The weighted variable group method was designed to diminish the emphasis placed on a few selected characters, or in other words, to provide a method for simultaneously considering many characters, as well as to diminish subjective bias in systematics. The data provided by such a method are therefore valuable in themselves. They may be used, furthermore, to aid in the recognition of genera of equivalent differentiation, so that the category "genus" means about the same thing in different parts of a group such as the *Hoplitis* complex, as indicated in the discussion of static relationships above.

Discussion and Conclusions

In the process of delimiting genera of modern organisms one may consider various factors such as the following: (1) relationships in a static, factual, or nonhistorical sense; (2) probable descent or phylogenetic relationships; (3) sizes of morphological gaps between any groups that might be recognized; and (4) the number of species in the groups.

Using static relationships based on numerous characters showing the amount of evolutionary divergence between any two forms, it is possible to organize species into a hierarchy of objective categories, or at least into categories more objective than those in general use. Once data for a revisional study of a group are gathered it is not prohibitively difficult or expensive to make such a quantitative study, since high speed electronic computers are becoming widespread. The method does not indicate how many categories are to be recognized, but if a horizontal generic line, for example, is drawn across the diagram of static relationships, the line will indicate groups of more or less equivalent distinctness, which may be regarded as genera. Raising the line will increase the number of genera, lowering it will decrease their number, but in any position the resulting categories will be approximately equivalent in evolutionary divergence.

It seems only logical and reasonable to accept such a relatively objective method in preference to the usual subjective methods for delimiting genera. However, most taxonomists in the zoological sciences, although perhaps not in botany, intuitively and without carefully differentiating types of relationships, place much more weight on phyletic than on static relations. Moreover, many systematists cannot escape the belief that the number of included species is an added major factor that ought to be considered in delimiting genera.

In my own experience I found a quantitative study of static relationships extremely valuable. In groups that lack excellent fossil records, static relationships provide the principal data available for use in judging probable phylogenetic relationships and sizes of gaps between groups. This is true, whether the data are treated statistically or subjectively, and whether many characters are used or only a few that are judged to be informative.

In a way a classification based on a phylogenetic diagram is a step beyond one based on a diagram of static relationships; the latter uses more nearly raw data. However, the former classification will fail to reflect accurately the amount of evolution among all forms. This is an important biological fact which I would like to show in addition to phylogeny. Although both cannot be shown in the same diagram, or indicated in the same classification, I believe that they should be independently indicated in revisional studies. In the past (Michener and Sokal, 1957), I have selected phylogeny as the main basis for the classification, and was glad to be able to indicate evolutionary divergence by means of static diagrams of relationships. Since the phylogeny is

subjectively determined in most cases, it did not disturb me to use, subjectively, other data to modify the classification based on it.

For example, amount of evolution modified a classification based on phylogeny (*Cubitognatha* is phylogenetically a species of *Rhamphorhina,* according to Figure 3, but so different as to merit a subgeneric name). Gap size might also have done so (a hypothetical example appears in Figure 5 A, where species *e* and *f* phylogenetically belong with *a* to *d,* but because of a gap due to extinction, would be placed with *g* to *n* in a classification). The number of species in a group would also influence its classificatory level. [*Proteriades* would have been included in *Hoplitis* (Fig. 3) had there been only a few species.]

These ideas meant, of course, that no straight line across a diagram of relationships could be used to define genera which are in any way equivalent. Of course a diagram of phylogenetic relationships, unlike one based on static relationships, has no significant ordinate except time (when known). Therefore it would be illogical to use with phylogenetic diagrams this method which can so well be applied to the weighted variable group diagrams.

These views can be summarized as follows: Static and phyletic relations are of equal interest to systematic biologists. In spite of their objectivity, it has seemed best not to use static relationships alone to construct a formal classification because it would be quite different from currently accepted classifications of many groups and because phylogeny has been the usually accepted basis for classifications in zoology. It has seemed preferable to me in the past to use presumed phyletic relationships as the main basis of classification, considering as secondary factors static relationships, number of species per group, and gap size. If this method is followed, the levels to which various units are assigned will continue to depend on the frequently differing judgements of authors. However, if autors can agree on probable phylogenies, the various possible classifications and different levels to which groups may be assigned need not be cause for great concern.

I believe that the need is for all systematists to publish with their works full statements of the type of relationships and other considerations behind their classifications. Only then will sufficient experience be accumulated to determine whether systematists as a group would be best advised to construct classifications based on static relationships, on phyletic relationships, or on some combination of these with other considerations.

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CHARLES D. MICHENER is Chairman of the Department of Entomology at the University of Kansas. This paper was presented at the Fourth Annual Symposium on Systematics at the Missouri Botanical Garden, St. Louis, Missouri. This Symposium was jointly sponsored by the Missouri Botanical Garden and the National Science Foundation.

Many of the ideas presented in this paper were clarified by discussion with Dr. Robert R. Sokal of the University of Kansas; some were original with him in one form or another.

Ontogeny and Systematics in Sponges

C. LEVI

THE systematics of the sponges stands out among that of other Metazoa because of the instability and variability of the large subdivisions of this phylum. This is probably one of the last phyla, the orders of which have not yet been precisely delimited. Before demonstrating that the observation of developmental processes can contribute information extremely valuable to an understanding of the relationships of the major subdivisions of the phylum, I should like to stress briefly their importance in specific determination.

Specific Determination of Sponges

Ever since the works of Schmidt and Bowerbank who pointed out the practical importance of the study of the skeleton, the majority of authors have established a sort of questionnaire for determination in which the study of spiculation occupies the predominant place. These are the principal criteria: form, size, color, consistency, surface, openings, anatomy, skeletal framework, skeletal details, locality, date. The respective importance of these different rubrics is extremely variable from one family to another, a fact which explains the profound differences among authors when they establish an order of priority for these diagnostic criteria. For Burton (1932) the list of types of spicules present is the most reliable guide for the diagnosis of the families; the disposition of the spicules in the skeletal framework and the small variations of form are the best criteria for generic distinction, while specific determination is based primarily on the external form of the sponge and sometimes on the shape and disposition of the spicules. The utilization of skeletal characters is then a supplementary method which is scarcely satisfactory for specific study. After a recent study of Mediterranean calcareous sponges, Sara (1951) reached the pessimistic conclusion that it was impossible to draw interspecific limits by the study of the form of the sponge or by that of the spiculation. This was doubtless the opinion of Vosmaer who united under the same name an unbelievable number of genera and species. Even Dendy, who knew the sponges in a particularly remarkable way, having studied them from diverse angles, ended numerous specific diagnoses with a question mark.

Only an approximate specific study can be made from the examination of even the most carefully assembled and preserved collections. Study *in situ,* (which is obligatory) makes the specific diagnoses easier, but more often than not, however, the study of form, if not of color, and that of skeletal elements is still insufficient. Recourse to histology and even to cytology is therefore necessary; even so, in a large number of cases, related species are still indistinct from these two points of view.

A combination of ecological and embryological data generally permits a resolution of the problem. The first type of data, which is indispensable, is easy to obtain; but this is not always true for the second type. Experience has, however, proved to me on several occasions that eggs and larvae of sibling species are different and that they permit recognition of such species pairs *a posteriori* (as in the example of *Octopus bimaculatus* Pickford and McConnaughey, 1949). Genetic criteria cannot be used in practice in sponges because of the phenomena of incubation, or the considerable difficulties of raising oviparous species which render crossbreeding impractical. It is only through the comparative study of development (and primarily of spermato-

genesis) that one can be certain of the validity of the species described. The embryological study of individuals of the same species collected in different regions reveals that their periods of reproduction may be somewhat out of phase, but the variability in larval morphology is so small that it does not in any case interfere with their identification. It is evident that this method is often impracticable and that it is, moreover, necessary only in certain border-line cases; but it is desirable to give data, however fragmentary, on the method of reproduction, which can serve as verification, and which will be, as we shall see, of considerable value for the establishment of a natural systematics of sponges.

Principles of Classification and Currently Used Systems

Beginning with 1862, a date which marks the appearance of the work of Schmidt, the systematics of sponges has undergone a series of transformations, which appear to be fundamental because of the multiplicity of names created by each new author, but which, if we group their essential aspects, can easily be summarized. In dealing with sponges, zoologists have found indeed but a small number of morphological characters which meet their taxonomic desires, namely characters concerned almost exclusively with the skeleton.

On the basis of the quality, quantity, form, and disposition of the skeletal structures, in spite of their variability, Schmidt had already been able to divide the sponges into six groups: calcareous sponges; horny sponges (with solid elastic fibers); siliceous sponges, globular in shape with a differentiated cortex; true siliceous sponges; and soft sponges without a skeleton. This basic conception of the classification of sponges remains entirely valid today, but subsequent research has shown that the divisions of Schmidt were of unequal importance and could not each retain the rank of class. The second classification of Schmidt, as a matter of fact, gives to each of them the rank of order.

After this first attempt based essentially on the *nature of the skeleton,* Lendenfeld and Vosmaer, opposing Calcarea and non-Calcarea, found that with the exception of this indisputable separation, the rest of the sponges could not so easily be divided into Cornea, Silicea, and Molla, and these two authors sought other criteria. In an effort to tackle this very problem, sponges collected by the "Challenger" were apportioned for study among several zoologists. The Calcarea were entrusted to Polejaeff, and the Acalcarea were divided, according to the *fundamental structure of the macrosclere,* among Schulze, who was responsible for the Triaxonida; Ridley and Dendy, for the Monactinellida; Sollas for the Tetractinellida; and finally, Polejaeff for the Keratosa without spicules. The results of these many studies led to the almost simultaneous elaboration of several general classifications, among others that of Sollas. The three classifications of Vosmaer, Lendenfeld, and Sollas isolate the Calcarea from the Acalcarea; among the Acalcarea, all three isolate the Hexactinellida. The rest of the sponges are variously distributed in several groups according to the fundamental structure of the macrosclere and the *form of the microsclere* (Fig. 1). Lendenfeld separates the Chondrospongiae with asteroid microscleres from the Cornacuspongiae with meniscoid microscleres; Sollas only uses microscleres to separate the Monaxonida with asters from those with sigmas or chelas, from those without microscleres at all. Vosmaer, who does not make use of microscleres, distinguishes only Spiculispongiae and Cornacuspongiae according to the *content of spongin* of the skeleton.

The systematics of sponges thus reached a level where it remained for a long time. Topsent borrowed fragments of these diverse classifications and was concerned chiefly with specific determinations, utilizing the division into Calcarea,

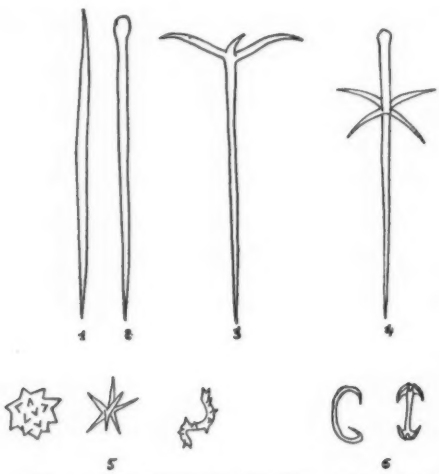


FIG. 1. Fundamental spicule types: 1, 2, monaxon megascleres; 3, tetraxon spicule; 4, triaxon spicule; 5, asteroid microscleres; 6, meniscoid microscleres.

Hexactinellida, Tetractinellida, and Monactinellida. Hentschel kept these diverse groups and separated from them only the Dendroceratida, thus following the erroneous example of Lendenfeld who had placed them near the Hexactinellida. It is to Dendy that we owe the last original contribution; for the division of the Demospongiae he used the nature of the microsclere *before* that of the macrosclere. This led him to divide them into Astrotetraxonida and Sigmatotetraxonida, thus regrouping into these two phylogenetic assemblages sponges as dissimilar as the Tetractinellida.

Thus, after a hundred years of systematic studies, the present classification of sponges recognizes the existence of three widely separated classes, the reciprocal relationships of which are completely unknown. These are:

a) Calcispongiae or Calcarea
b) Hyalospongiae or Hexactinellida
c) Demospongiae or Corneosilicea.

Within the class Demospongiae, one can distinguish two subclasses corresponding more or less exactly to:

Spiculispongiae and Cornacuspongiae (Vosmaer)

Chondrospongiae and Cornacuspongiae (Lendenfeld)

Tetraxonida and Cornacuspongiae (Hentschel)

Astrotetraxonida and Sigmatotetraxonida (Dendy)

We will now consider the composition of these two subclasses.

The Cornacuspongiae or Ceractinella are defined by Vosmaer as sponges with monaxon spicules more or less imbedded in spongin, or if without spicules with the spongin developed and sometimes containing an appreciable number of foreign bodies: Lendenfeld adds that the spicules are never tylostyles and that the microscleres, if they exist, are never asteroid. The existence of spongin and its enormous development in the group of Cornacuspongiae is the principal fact which has since held the attention of all zoologists; but Vosmaer and Lendenfeld recognized that the separation of the Demospongiae into two large assemblages based on this criterion is not absolute. I shall consider, therefore, as Cornacuspongiae an assemblage of sponges, the siliceous skeleton of which, if present, is formed of megascleres which are always monaxonids, of microscleres which are never asteroid, and of fibers of spongin which can attain at times a very high degree of development. Of course, if the sponge has no microscleres and has only a little spongin, there is the risk, according to this definition, that it can be placed as well in this group as in the other, and we can do nothing about it. To the Cornacuspongiae belong the horny sponges, Keratosa or Ceratina, and the three orders of siliceous sponges defined later by Topsent under the names of Haplosclerina, Poecilosclerina, and Halichondrina.

To this homogeneous assemblage whose subdivisions are very poorly delimited, all authors oppose that of the Spiculispongiae or Chondrospongiae. This group unites sponges whose skeletons are composed of asteroid microscleres and of monaxonid or tetraxonid megascleres which are generally not cemented by spongin. These

are principally the Tetractinellida and Hadromerida. To the Spiculispongiae also belong some sponges difficult to classify like *Tethya, Chondrosia,* and *Oscarella,* for which Vosmaer had created the suborders of Pseudotetraxonida and Oligosilicina. Finally, a whole assemblage of sponges in which the siliceous spicules are arranged in a rigid skeleton by fusion of their extremities, constitutes the suborder Lithistida, doubtless related to the Tetractinellida. The Chondrospongiae of Lendenfeld differ from the Spiculispongiae of Vosmaer by the inclusion of the Axinellidae and Spongillidae.

Pitfalls in the Preceding Classifications

From this brief survey of the various systems for sub-dividing the Demospongiae, we see that these divisions, established to meet the needs of different systematists, correspond roughly to those which can be proposed empirically in the light of embryological results known at present.

What are the difficulties that most systematists have encountered in their attempts at a natural classification? In the first place, the existence of sponges without a skeleton, which are obviously impossible to group in a classification based on spicules, except as an assemblage with negative, and at the same time heterogeneous, characters. These constitute the order of Oligosilicina or Myxospongiae, comprising *Chondrosia, Oscarella,* and *Halisarca,* genera with diverse and very dissimilar affinities.

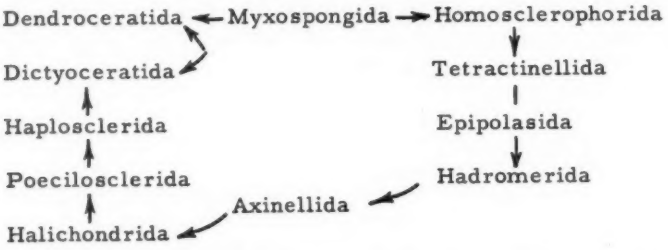
A number of sponges with a reduced or dendroid horny skeleton, at present united in the order Dendroceratida, have similarly undergone frequent transfers, while remaining grouped together. The most extraordinary transfer is doubtless that made by Lendenfeld, who placed them close to the Hexactinellida under the name of Hexaceratina, on the basis of the tubular structure of the flagellated chambers and on the unusual presence in *Darwinella* of horny fibers in the form of triaxon "spicules." Despite their great similarity in constitution to other horny sponges, Hentschel continues to isolate them, separating them completely from the Cornacuspongiae and giving them an importance equal to that of the Hexactinellida. But, on the other hand, many authors, while admitting their autonomy, relate them to the horny sponges with a reticulate skeleton, and place them in the middle of the Keratosa, thus in the Cornacuspongiae (de Laubenfels, 1950).

The Halichondrina in the sense of Topsent, and especially the Axinellidae, constitute a new assemblage of sponges, the systematic position of which is often disputed. The difficulty here stems from too great a simplicity in the form of the spicules. Vosmaer places them in their entirety in the Cornacuspongiae; Lendenfeld, on the contrary, divides them and places the Axinellidae among the Chondrospongiae. Through their monaxon spicules and the presence of spongin in variable quantity, the Axinellidae seem to belong to the Cornacuspongiae, but their radial skeletal framework as well as the existence of related forms with asteroid microscleres (e.g., *Hemiasterella* and *Adreus*) relates them to the Tethyidae and Suberitidae. It is, in general, by way of the Axinellidae that authors have derived all the Cornacuspongiae from a stem with tetraxonid spicules. But in reality—as I shall explain further on, in agreement with Lendenfeld on this point—the separation between the two large groups is created by the inclusion of the Axinellidae in the Chondrospongiae.

Finally, and the last subject of discussion, the Plakinidae and related genera with spicules of small size are isolated within the Tetractinellida, and the genus *Oscarella* which lacks a skeleton is closely related to them. The structure of the amphiblastula larva, which has been known for a long time, has led different authors to see in the Plakinidae the basic stock of the Demospongiae.

I shall summarize in Table I the present state of the discussion based exclusively on the results of systematists.

TABLE I—PRESENTLY ACCEPTED RELATIONSHIPS BETWEEN MAJOR GROUPS OF DEMOSPONGIAE



It stands out clearly that the Demospongiae are grouped into two large assemblages of which the only points of contact are the Myxospongida and especially the Axinellidae; but the embryological results previously mentioned will permit us to support the hypothesis of their complete independence.

Ontogenetic Classification

The utilization of ontogenetic characters for the understanding of systematic problems in sponges has been employed successfully by both Maas and Topsent, in the limited case of the Cornacuspongiae. The study of larvae convinced Maas of the close relationship of the horny and corneosiliceous sponges, and Topsent of the existence of several natural groups of halichondrines. Both insist on the importance of ciliature and larval pigmentation.

Furthermore, it has been long known that the larva of *Oscarella,* a sponge without a skeleton, is a hollow amphiblastula (Fig. 2) and that it resembles the larva of *Plakina,* an aberrant tetractinellid. All the other known larvae of the Demospongiae are solid parenchymellas (Fig. 2) and are incubated, with the exception of the larvae of *Cliona stationis* (Nassonow) and *Tethya* (Nagai), which are oviparous sponges. I have made a detailed comparison of the development of *Oscarella lobularis* (O. S.) and of another sponge without a skeleton, *Halisarca dujardini* Johnston, of doubtful systematic position. This comparison which was made in order to utilize ontogenetic facts for systematic purposes has yielded the following results (Fig. 3):

a) These two species have larvae of different types (amphiblastula and parenchymella) and the metamorphosis of each progresses according to a different scheme.

b) The development of *Halisarca* closely resembles that of certain horny sponges and hence of the assemblage of Cornacuspongiae.

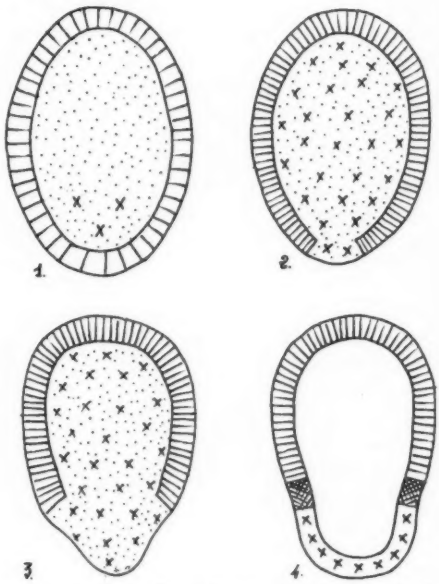


FIG. 2. Larvae of Demospongiae: 1, 2, 3, three types of parenchymellas; 4, amphiblastula.

Hatching: external larval cells destined to become internal after metamorphosis. Crosses: internal larval cells responsible for the formation of adult ectomesenchyme.

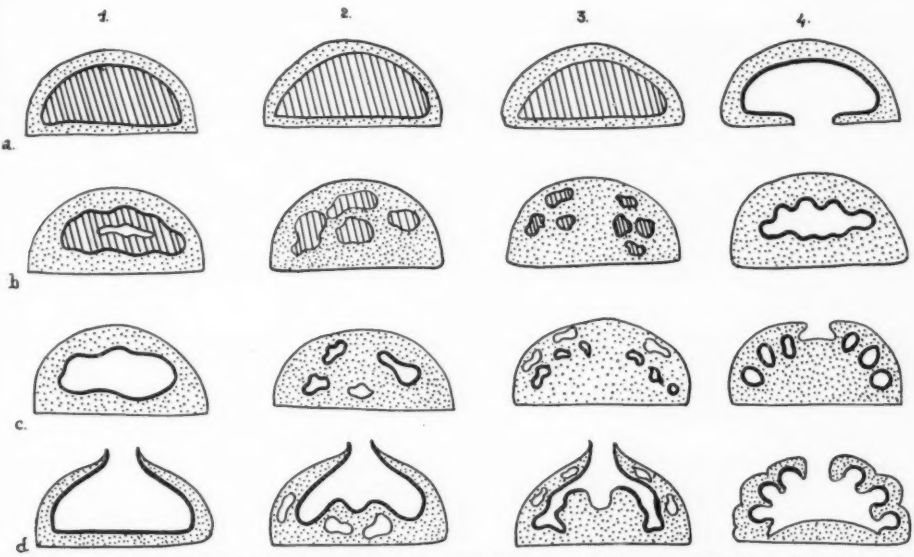


FIG. 3. Metamorphosis and adult histogenesis in 1, *Halisarca dujardini* Johnston; 2, *Halisarca metschnikovi* Lévi; 3, *Aplysilla sulfurea* Schulze; 4, *Oscarella lobularis* (Schmidt). *a*, fixation of the larva; *b*, formation of choanocytal masses; *c*, formation of cavities; *d*, rhagon.

c) This development is the simplest known in the Demospongiae and results in the formation of a sack with double walls, opening by an osculum, that is, an asconoid rhagon.

d) A sibling species of *Halisarca dujardini*, discovered in the course of this study, differs from it in forming an almost syconoid rhagon, and thus resembles *Aplysilla*, a recognized horny sponge, of which the rhagon is typically syconoid.

A comparative study extended to the assemblage of the Cornacuspongiae shows that the precise study of embryogenesis, of larval structure, and particularly of adult histogenesis (formation of the rhagon) provides information about interspecific relations and permits us to outline new hypotheses on the evolution, from their early stages, of sponges constructed on the general leuconoid type. All the Cornacuspongiae studied (with a few exceptions, the importance of which we shall see later on) possess incubated parenchymella larvae of large size (100 micra to several mms). The discovery of new interspecific or intergeneric relationships which ontogenetic study reveals, entails revision in the details of the large orders established by Topsent. The essential outlines of his classifications which resulted from the use of classical morphological methods remain entirely valid.

The two cases of known oviparity indicated above (*Cliona* and *Tethya*), concerned Demospongiae Spiculispongiae. The study of numerous species of sponges belonging to different families of Spiculispongiae has convinced me of the generality of the phenomenon of oviparity in this group. The study of the development of *Tethya* and *Raspailia* indicates, moreover, that:

a) the eggs after laying have relatively small dimensions and scantier yolk reserves in absolute terms than those of incubated eggs of the Cornacuspongiae,

b) the free larva of the parenchymella type, which develops rapidly (i.e., its larval histogenesis is short) is much richer in reserves than is the larva of Cornacuspongiae (Fig. 4),

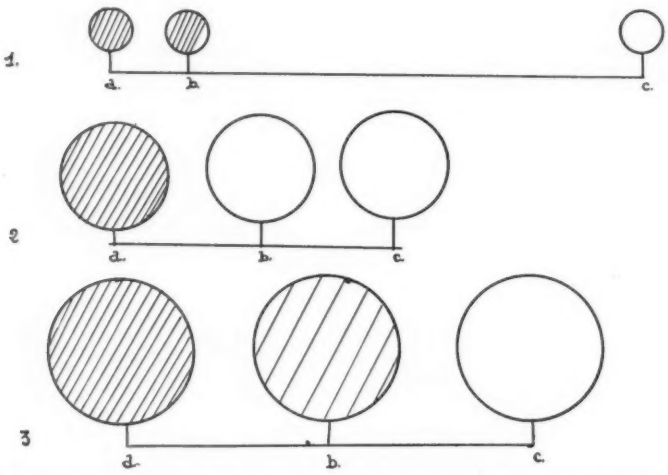


FIG. 4. Comparison of the development of *Halisarca*, with incubated parenchymella, and that of *Tethya*, with free parenchymella. 1, *Tethya aurantium* (Pallas); 2, *Halisarca dujardini* Johnston; 3, *Halisarca metschnikova* Lévi.

a, duration of larval histogenesis; *bc*, duration of adult histogenesis. Yolk reserves are indicated by hatching.

c) adult histogenesis seems to be extremely long, as opposed to that of the Cornacuspongiae which only lasts three to eight days.

Almost all the sponges studied, the oöcytal characters of which agree with those of *Tethya, Cliona,* or *Raspailia,* belong to the two orders of Hadromerida and Axinellida. Sexual reproduction in the Tetractinellida, which represents a large part of the Spiculispongiae, is almost totally unknown, and the presence of sexual products in these sponges, as occasionally reported, should be viewed with caution, if not skepticism. Only *Oscarella* and *Plakina* are distinguished by incubated larvae of the amphiblastula type.

Summarizing all known ontogenetic observations and without having recourse to morphological studies of the adult one can divide the Demospongiae into:

a) Cornacuspongiae with an incubated parenchymella larva,

b) true Tetractinellida with sexual reproduction still unknown,

c) aberrant Tetractinellida (Homosclerophorida, *Oscarella,* etc.) with incubated amphiblastula larva,

d) oviparous Hadromerida and Axinellida with parenchymella larva.

Proposed Classification—Possible Phylogenetic Relationships

To judge the real value of these results, and therefore the importance of the embryological criteria used, it is indispensable to refer to the classical morphological classifications (i.e., those of Sollas, 1888; v. Lendenfeld, 1889; Dendy, 1921; Hentschel, 1923; Topsent, 1928; and de Laubenfels, 1936.) In each classification, one can indicate for each of the families the mode of reproduction as follows: large incubated eggs, parenchymella; large incubated eggs, amphiblastula; small eggs, oviparity, parenchymella; or reproduction still unknown.

It is immediately apparent from examinations of the classifications of Sollas, Lendenfeld, and Topsent that the superposition of the morphological and embryological facts is rather astonishing. One can draw several conclusions:

1) With the exception of certain fami-

lies about which we have no information (but which are related to families of known reproductive habits), it is possible to group the Demospongiae into four assemblages of unequal value. The most homogeneous group is the one which includes the Cornacuspongiae of Lendenfeld; the Ascomorpha and Meniscophora of Sollas; the Poecilosclerida, Haplosclerida, and Ceratellida of Topsent. We shall call these sponges the Ceractinomorpha. On the other hand, we shall group provisionally under the name of Tetractinomorpha, the Chondrospongiae of Lendenfeld (with the exception of the Spongillidae). But, basing our conclusions on embryological data, we shall, like Dendy, group the Oscarellidae, Plakinidae, and Corticiidae into the Homosclerophora. Under the term Choristida we shall keep the Astrophora and Sigmatophora to which we shall add the Chondrosidae and Chondrillidae. We shall reserve the new term of Clavaxinellida for the assemblage of Hadromerina and Axinellidae which certainly have closely similar origins. There remains the group of families with an ill-defined spiculation composed chiefly of oxeas and asters, which we shall rank in the order Epipolasida until more is learned about them.

2) The Axinellida occupy rather different positions in the classifications of Lendenfeld, Sollas, and Topsent, a situation which is the result of the simplicity of their spiculation.

3) The Desmacellinae, isolated in the midst of the Cornacuspongiae and the Poecilosclerida, are in reality very close to the Axinellidae, as Hallmann (1916) has already shown, but one must separate *Tylodesma* (*ex Desmacella*) from certain *Biemna* with mycaline affinities, with which they are generally united because of the convergence of their spiculation.

4) The morphological criteria used by the three authors are therefore essentially valid; the main ones are the form of the spicules—tetractines, tylostyles, or others; and the presence of microscleres, asters or chelae.

Dendy's subdivision of the sponges into two phyletic lines based on the presence of chelaes or sigmas proves incompatible with embryological classifications. The choice of the sigma as a major criterion is in effect not justified, for the sigma exists in numerous very different sponges and does not have the same origin in all cases (arising from microxeas, toxas, chelas, etc.). The new plan of classification of the class Demospongiae is given in Table II.

It is necessary to keep in mind the fact that the five orders of Ceratinomorpha are so closely imbricated that there is no doubt about their common origin. On the other hand, the diverse orders of the Tetractinomorpha will doubtless be separated some day into two new subclasses, one tetraxonid, the other monaxonid, or rather, as Vosmaer stated, pseudotetraxonid. So it is advisable not to expect that each of the ten orders of the Demospongiae will have the same value.

To conclude this systematic study of the Demospongiae, it seems to me desirable to indicate my point of view concerning the phylogenetic relationships of the different groups, as based upon the three sources of information—cytological, anatomical, and embryological. In this discussion, I shall consider as more complex that organism which is distinguished from the others by the indisputable specialization of its adult structure and its processes of morphogenesis.

TABLE II—PROPOSED CLASSIFICATION OF THE DEMOSPONGIAE

CERACTINOMORPHA	TETRACTINOMORPHA
Dendroceratida	Homosclerophorida
Dictyoceratida	Tetractinellida
Haplosclerida	Clavaxinellida: Epipolasida, Hadromerida, Axinellida
Poecilosclerida	

My essential position rests in this statement that the Demospongiae represent an assemblage of at least two lines of sponges, the evolution of which, from a very ancient and unknown stock, has unfolded in parallel paths, resulting in the development of species which sometimes exhibit striking convergence.

It seems reasonable to look for primitive sponges among those whose cellular elements remain relatively little differentiated, which lack a skeleton, and in which the embryology, or better, the first adult stage, i.e. the rhagon, offers to the observer a minimum of complications. It is easy to see within the genus *Halisarca* some ceractinomorph species that could be close to this primitive state. On the other hand, one must be more cautious in asserting that *Oscarella* is very near the primitive tetractinomorph stock. Indeed, the embryological stages of *Oscarella* are more complex, while the adults remain at a level of structural organization much simpler than that of any other tetractinomorph sponge. This is why, until the possible discovery of small, amorphous sponges, without a skeleton, and composed of a double cellular layer in which the cells would be equivalent, I shall consider *Oscarella* and *Halisarca* as the most primitive of sponges known at present.

The different orders of the subclass Ceractinomorpha are so united with one to another that it is difficult to establish their exact relations, but it is very likely that beginning with a common origin near *Halisarca,* the first degree of complication is achieved in the Dendroceratida, the aquiferous structure of which is relatively simple; the formation of spongin, which has increased in the closely related Dictyoceratida, is equally manifest in the Haplosclerida which also take up silica, and use it to form the simplest spicule, the pointed rod or oxea.

Numerous Poecilosclerida still produce spongin, but one cannot be certain whether these are derived from a dictyoceratid or a haplosclerid stock, or more likely, from both simultaneously. The last stage of the Ceractinomorph series must be sought among the Halichondrina, but it remains very evident that *Hircinia, Spongia, Mycale, Microciona,* and even *Adocia,* are just as, if not more highly developed, than *Hymeniacidon.*

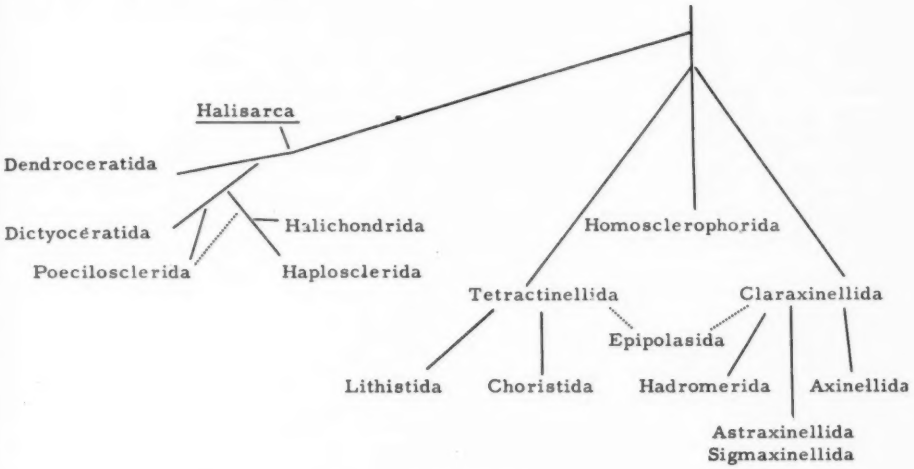
The beautiful studies of Minchin, Dendy, and Hentschel on the evolution of the spicules of sponges, allow one to affirm that the megasclere always passes through the oxea stage before attaining the style (or other) stage and that the evolution of the microsclere always follows the series: microxea; toxa or sigma; chela, equal and then unequal. And we assert that this confirms the speculations drawn from embryological arguments.

The evolution of the Tetractinomorpha is much more obscure by reason of its possible double origin. Classical theory makes the following derive successively from *Oscarella:* Tetractinellida, Hadromerida, Axinellida. The fundamental spicules of this subclass are the triaene, oxea, and aster, and certain persons think they have found in the order Homosclerophorida, among species related to *Oscarella,* sponges with spicules having a number of variable oxeas, which would permit making them the basic common stock. Perhaps this is the best solution. I do not believe so, however. Among the Tetractinomorpha there are three tendencies: one with the development of the triaenes, the others with the oxea and style. The evolution of the aster is secondary. One has sought to discover all the stages of transition between the Homosclerophora and the other Tetractinellida without really arriving at this end, and I have recently (1953) affirmed my position with regard to this matter.

The evolution of the Tetractinomorpha has proceeded along different lines with tendencies to a massive or globular form, to a radial or axial skeletal framework, and in individual cases to the develop-

ment of the triaene, oxea, or style. The small order of Homosclerophorida which presents these diverse tendencies, is not the common origin of the Tetractinomorpha, but remains entirely problematical and perhaps quite distant from that of the Tetractinellida.

Finally, I shall set up the following table of the phylogenetic relations of the Demospongiae:



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C. LEVI is chief of research at the Biological Station at Roscoff, and lecturer at the Faculté des Sciences, Strasbourg. In addition to his investigations into the ontogeny and systematics of sponges, he has studied the interstitial microfauna of marine sands. The assistance of Willard D. Hartman, sponge expert at the Peabody Museum, Yale University, in the translation of this paper is gratefully acknowledged.

The English Word "Nema" Revised

B. G. CHITWOOD

MANY years have passed since Cobb (1919) published his article on the classification of the phylum "Nemates." He had previously (1917) used the word "nemas," though, in the same article, the word "nematodes." In 1931 he published an excellent diagnosis of the phylum in his presidential address before the American Society of Parasitologists and in 1932 used a title here included in the title of this article—namely "The English word 'nema,'" explaining the derivation of the word "nema" and proposing various derivatives from it.

As Cobb pointed out, the term "nematode" is a contraction or vulgarity for nematoid and a weaker term since it means "thread-like," while nema means "thread." In the same article he published various derivatives of the word nema, i.e., "nematicide," "nematosis," "denematize," and pointed out the value of their usage.

Zoologically speaking, the vernacular word "nematode" is a corruption of the ordinal name NEMATOIDEA of Rudophi (1808, pp. 197, 198). It was already in use—in its German plural equivalent "Nematoden"—at least by the time of Wiegmann (1835, p. 336), who, however, continued "Nematoidea" for the taxon itself. Beginning with Burmeister (1837, *n.v.*), the stem *nematod-* was used by some workers for a formal zoological group—in Burmeister's case for a *Familie* NEMATODES.[1] Subsequently, both R. Leuckart (1848, p. 77) and von Siebold (1848, p. 112) employed an *Ordo* NEMATODES, which Diesing (1861, p. 598) modified to *Ordo* NEMATODA. Vogt (1851, p. 174) first proposed the name NEMATELMIA for a *Klasse* to include the *Ordnungen* NEMATOIDEA, GORDIACEI, and ACANTHOCEPHALA. This name was modified to NEMATHELMINTHES by Gegenbaur (1859, p. 137) and NEMATELMINTHES by Carus (1863, p. 456). Later, both NEMATOIDEA and NEMATHELMINTHES were promoted to phylar rank. Since the grouping of nemas, horse-hair worms, and thorny-headed worms (acanthocephalans) has never been a sound zoologic concept, the names Nematelmia, Nematelminthes, and Nemathelminthes should be dropped, as they have been by most thinking zoologists in recent years.

As originally proposed by Rudolphi (1808, 1809), the order Nematoidea contained some species that were originally described as gordiids (horse-hair worms) and that later workers placed in synonomy with gordiids. Von Siebold (1843, p. 302) created an *Ordnung* GORDIACEI, coordinate with the *Ordnung* NEMATOIDEA, but incorrectly associated the nemic genus *Mermis* with the horse-hair worms of the genus *Gordius*. This continued to be true for much of the remaining half of the 19th century. Huxley (1864, p. 47) promoted the horse-hair worms provisionally to a *Class* GORDIACEA, coordinate with a *Class* NEMATOIDEA in a category SCOLECIDA (which he treated as a class, or alternatively as some unspecified higher category containing the classes Nematoidea, Gordiacea, etc.). However, it appears probable, on the basis of later publications by him (Huxley, 1877, p. 641, in which he reverted to a group NEMATOIDEA—of unspecified rank but containing as "Groups" Polymyaria, Meromyaria, and Holomyaria, in the last of which he included *Gordius*), that in 1864

[1] Inappropriate; the Greek adjective: nominative singular, *νηματώδης* (m.,f.), *νηματῶδες* (n.); nominative plural *νηματώδεις* (m.,f.), *νηματώδη* (n.)—of which the most probable Latin equivalent would have been: sing. *nēmatōdēs* (m.,f.,n.); pl. *nēmatōdēs* (m.,f.), *nēmatōda* or *nēmatōdia* (n)—means *in filaments, filamentous.*

he had no better concept of the Gordiacea than had von Siebold in 1843. Such was equally the case with Lankester (1877, p. 449), who promoted the NEMATOIDEA to the level of *phylum*, but included therein, as a "subdivision," the GORDIIDAE. The first clear distinction between the nemas and gordiids was realized by Vejdovský at which time he named a group to contain the horse-hair worms the order NEMATOMORPHA (1886, Řád [=Order], p. 634).

There is no question that Cobb first proposed the Phylum Nemates in 1919 and gave a diagnosis in 1932. The fact that Potts (1932) and the writer in 1950 did not recognize Nemata Cobb, 1919, but rather synonymized it with the Nematoda (as a phylum) is lamentable. We can only say that the writer was young, foolish, and ignorant and did not realize the far-reaching importance and soundness of Cobb's work. The values of the derivative words and, in particular, the saving in time of secretaries and clerical workers and in costs of publication resulting from the shortening of "nematoid" or "nematode" to "nema" were not impressed on him at the time. If he had realized that the group was a sound phylum when the first part of "An Introduction to Nematology" was written starting in 1937 (see Chitwood, 1937, 1940), and particularly if he had paid proper heed to Cobb's work when preparing the revised edition, which appeared in 1950 (see Chitwood, 1950), this article might not be necessary. He can only plead ignorance and request all good people to drop that corrupt word nematode, remember, of course, that they are not toads (even though a farmer once asked what kind of toads they were), and thus not use it in polite company!

The following is a reproduction of Dr. Cobb's (1932) article, which is out of print and written much better than the author could write it:

For thousands of years the word 'nema' has been a household word—the Greek word for 'yarn' or 'thread,' and was introduced, unaltered, into Latin. As a suffix it enters into a large number of English technical words (less often, as a prefix) and as such has a place in all large dictionaries.

The word 'nema,' meaning a nematoid or nematode, has been used for some years in the publications of a number of reputable authors, and its use is increasing, largely, no doubt, because it lends itself very readily to the formation of euphonious derivatives having precise and obvious meaning—words widely useful in the literature of parasitology and medicine. 'Nematologist' and 'Nematology' are established words in the business of the U. S. Department of Agriculture and occur in acts of Congress.

This use in English of the word 'nema' by itself is simply a slight modification of the usage of generations of scholarly naturalists who have coined such words as Pontonema, 'sea nema,' coined by Leidy, Ichthyonema, 'fish nema,' coined by Diesing, and Allantonema, 'sausage-shaped nema,' coined by Leuckart.

This is such well established usage that there are well toward a hundred genera of nemas whose names end in the syllables 'ne-ma.' In following and extending this long-established custom, one is simply accepting a metaphorical use of the word 'nema,' so that it is in reality only a slight and obvious step to admit it in this form as a common English word. Not only does it lend itself readily to the formation of useful derivatives but it is preferable to 'nematoid' or 'nematode' in that it is shorter and makes use of a more forceful form of speech, the metaphor. The word 'nema' has more force than 'nematoid' in accordance with the general law that the metaphor is more forceful than the simile. An obstinate or stupid person is said to be 'asinine' (simile) but, far more forcibly, is said to be an 'ass' (metaphor). In a similar way it is more forceful to call an organism a 'thread' (nema) than to call it 'threadlike' (nematoid), and here, as usual, the metaphor is the shorter form. The plural 'nemas' is preferred to 'nemates,' just as 'lemmas' is preferred to 'lemmates' and 'edemas' to 'edemates.'

DERIVATIVES OF THE WORD NEMA

The following are useful, practically self-explanatory, derivatives:

Nemic, of or relating to nemas. Formed as in the words 'anemic' and 'systemic,' preferred to 'nematic' or 'nematical,' which, though 'purer,' are more clumsy.

Nematology, the branch of zoology dealing with nemas.

Nematologist, one versed in nematology.

Nematize, to populate or infest "[= infect [2]]" with nemas.

Denematize,* to divest of nemas.

Nematization, the state of being populated or infested "[= infected [2]]" with nemas.

Nematosis, a morbid condition due to the presence of nemas.

Nematicide,* a substance or thing fatal to nemas.

* The Latins took over the word 'nema,' declining it as in the Greek, and this Romanization may justify the combinations 'denematize' and 'nematicide.'

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B. G. CHITWOOD is Chief Nematologist, State Plant Board of Florida, Gainesville. This article represents a synthesis of recent developments in the field of Nematology and includes corrections of previous errors. In the preparation of this work the author has been permitted to take time from his regular duties with the State Plant Board of Florida and has had the use of the Biology Library on the Berkeley campus of the University of California. He has had help from Dr. M. W. Allen, Associate Professor of Nematology, and from Dr. Ellsworth C. Dougherty, Director of the Laboratory of Comparative Physiology and Morphology of the Kaiser Foundation, University of California, Berkeley. However, the author takes responsibility for the views expressed in this article, which do not necessarily reflect those of friends or associates.

[2] The present writer (B.G.C.) prefers to follow Dropkin (1955) and the recommendation of the Report of the Committee on Terminology of the American Society of Parasitologists (Hertig *et. al.,* 1937) with respect to the usage of "infect" and "infest." The terms "infect" and "infection" are used for those nematodes [sic] that invade and establish (maintain) themselves within the body of the host, whereas "infest" and "infestation" refer to external parasites, which maintain themselves on a host. Nonliving material, i.e., soil, can only be infested. to which purists might object.

[3] Not seen.

Chordate Phylogeny

G. S. CARTER

THE ORIGIN OF VERTEBRATES. By N. J. Berrill. Oxford University Press. London. 1955. viii+257 pp., 31 figs. 25 shillings.

THE phylogeny of the chordates is a classical subject of zoological speculation. Theories concerning it may be, as Professor Berrill says, 'such stuff as dreams are made on,' but there can be no question of their perennial fascination for zoologists. It is then pleasant to be given a re-discussion of the subject on modern data by an expert on one of the groups most closely concerned, the Urochordata.

Professor Berrill summarises much of the knowledge of the morphology, embryology and bionomics of the urochordates that has resulted from his researches during the last thirty years. Here, it is not open to one who lacks his expert knowledge to criticise, but in working out his theory of chordate evolution he raises many points of general biological interest, and these a general biologist may, perhaps, be allowed to discuss. It will be found that in all the points discussed in this article I am unable to agree with his arguments and conclusions, but this must not be taken to imply that I think the book valueless. His summary of the biology of the urochordates will be most valuable to all readers who are not expert in the group, and, though I suspect that at many places the evidence he uses to build up his theory will seem insufficient to justify his conclusions, there can be no doubt that his treatment of the subject is full of interest. The book should certainly be read by every one who is interested in the origin of the vertebrates.

(1) Professor Berrill gives us many interesting details of the adaptations of various ascidian tadpoles to settling in positions suitable for the life of their respective adults. He shows that both their sense-organs and their behaviour are adapted to this end. But he then proceeds to maintain (e.g. pp. 36, 67) that this is evidence that the tadpole is a caenogenetic stage introduced into the life-history of the ascidian for this purpose. So far as the fundamental structure of the tadpole is concerned, this seems to me a *non sequitur*. When an animal organism or organ becomes adapted to some new function, it normally retains its previous basic organisation and only the relatively superficial details of its structure are altered. Our own arms and hands are beautifully adapted to hold and manipulate objects outside the body, but we do not say that they were therefore evolved for this purpose by caenogenesis at the stage at which they became so adapted. We know that they retain the fundamental structure that they possessed when the arm served as a supporting limb; only the form and use of the previously-given parts are modified. Every zoologist knows that similar examples occur throughout the animal kingdom—the whale's tail retains the fundamental structure of a mammalian tail in its segmentation and so on, though now modified for the new function of swimming; the bee's sting is a modified ovipositor; the cephalopod funnel shows its origin in the molluscan foot. In evolution organs are undoubtedly sometimes evolved *ab initio*, without antecedents, but not all or even the majority are. It seems to me that we should never claim caenogenetic origin for the basic structure of an organism or organ unless we have direct evidence. I do not think that the adaptations of the ascidian tadpole provide any good evidence that its fundamental structure is caenogenetic.

(2) Professor Berrill suggests (p. 69)

that the tail of the tadpole evolved suddenly as the result of a mutation that caused vacuolation and enlargement of the cells of the notochord, whereby it was elongated beyond the former body and gave rise to a tail. The muscles, he thinks, were drawn out with the tail. If this was the course of the evolution, we should have here an ideal example of Goldschmidt's 'hopeful monsters.' But I think few modern students of evolution have accepted that such large and sudden changes are a probable basis for evolutionary advance. Apart from the difficulty of understanding the persistance of a single large mutation, even though it were adaptive, it should be appreciated that before a suddenly-formed organ could be useful, and therefore of selective value, much other change in the body would be necessary—in the case of tail new patterns of behaviour would be needed to enable it to be used as a locomotory organ—and the theory of 'hopeful monsters' does not explain how these other changes are brought about at the right moment. A gradual evolution is far easier to understand, and it seems to me that evolution by hopeful monsters should not be postulated in discussions of phylogeny until this type of evolution has won a place in the accepted theories of evolution.

(3) In places (e.g. pp. 63–4) Professor Berrill compares the process of bud-formation with that of the development of the egg as if the two were comparable as being different forms of the same process, though it is true that he notes that bud-formation is direct and development often indirect—as it is in many urochordates. To me any comparison is unjustifiable; I think we have no evidence that the two are forms of the same process. I believe rather that there are two quite distinct ways in which the adult form is reached in the animal body. One is development from the egg to the adult and the other is the attainment of the adult form seen in regeneration, redifferentiation, restitution and bud-formation. The latter is in essence a direct moulding of the tissues. It is most clearly distinguished from development in being direct; it shows no sign of adaptation to different environments in the course of its progress—a polychaete bud does not show any signs of the special organs of the trochophore, nor an ascidian bud such organs as the tail of the tadpole.

The formation of the neural groove in the stolon of *Salpa*, which Berrill describes (p. 63), might at first sight seem contrary to this view, for it forms in much the same way as in the tadpole larva of other urochordates, and is not a direct moulding into the form of the adult's ganglion. But it should be remembered, first, that the stolon is not a bud but an organ from which a large number of buds arise, and for this reason the mode of formation of its neural groove may seem hardly relevant to bud-formation. Secondly, even if this is not accepted as decisive, the stolon is an embryonic organ and the development of the neural groove may be reminiscent of the structure of an ancestral tadpole stage now lost, for buds are known to reproduce the stage of the life-history at which they are formed.

However this may be, it seems to me that the great mass of available evidence shows that the development of the egg and the moulding of a bud into the adult form, should, in the present state of our knowledge, be regarded as entirely different processes. I suggest that for the sake of clarity the term development should be restricted to that of the egg in sexual reproduction. If my view is accepted, the facts of bud-formation cannot be used to throw light on the phenomena of development.

(4) Professor Berrill thinks that the euchordates must have migrated into the fresh waters shortly after their separation from the urochordate stock. That they did so migrate at some stage must of course be accepted, but I do not see on what grounds we need to believe that the migration was so early, and not at a much later stage such as that represented

today by *Amphioxus*—why indeed the latter may not be primitively marine.[1] Berrill then insists that migration up the rivers would have required the evolution of improved locomotory powers that is evident in the euchordate line of descent. I do not think that any very active swimming is required for such a migration, for we know that the Cambrian waters, in which the migration is supposed to have taken place, contained a rich flora of sessile algae (Seward, 1931, pp. 101–9). Among such vegetation there must have been many opportunities for migration through waters of negligible current.

However, whether active locomotion was necessary for the migration or not does not seem to me important for the development of Berrill's theory, for there can be no doubt that one of the characteristics of euchordate evolution was the development of improved locomotory powers.

(5) I want to discuss in somewhat greater detail the necessity for believing in a sessile stage in the evolution of the euchordates, and for believing that neoteny occurred in it. Both of these beliefs are required by Professor Berrill's theory.

His interpretation of the evolution is that in an early urochordate a stage of the life-history shortly after settling become neotenous and returned to a free-swimming habit. His reasons for these conclusions are discussed below.

I take it that the present-day conception of the evolution of the animal life-history is that it evolves by adaptational change at all its stages but that, except in special cases such as those in which the egg comes to contain a large amount of yolk, the changes are greater in the later parts of the life-history. For this reason larvae of related animals are more similar than are the adults. I assume that the theory of recapitulation—evolution by the addition of new stages at the end of development—is not now accepted as at all generally true of evolution. Resemblances between animals, larval or adult, remain of evolutionary significance even though the evolution is not recapitulatory, but the larva of a later form represents the ancestral larva, not the ancestral adult. What the ancestral adult was like before its modification into the present-day forms, we are usually unable to say, except in the most general terms, unless we have fossil evidence of its characters. My discussion is founded on the basis of these views. I have thought it worth-while to introduce this paragraph since I cannot be sure that Professor Berrill accepts them in their entirety (cf. p. 42).

No one, I think, will question that the urochordates and euchordates are related groups and descended at some stage from a common ancestral stock. I think also that it will be admitted that the urochordates must have evolved from a free-swimming, non-sessile group of animals, since sessile habit cannot be supposed to be primitive in bilateral animals such as the chordates. We can only say very generally what were the characters of this non-sessile ancestor of the urochordates, but it seems to me natural to suppose that it had a tadpole larva—in contradiction to Berrill's belief that the tadpole is caenogenetic, the grounds for which, as I have said, seem to me insufficient—and an adult condition not unlike the tadpole larva in general structure but larger and with the more complex structure that goes with larger size in a free-living animal. This seems probable for a primitive life-history is likely to have been direct, and we are assuming the habits of larva and adult to have been similar.

The great resemblances between the structure of the tadpole larva and that of the simplest euchordates show, I think, that the common ancestor of the uro- and

[1] Berrill holds (p. 189) that the presence of nephridia in *Amphioxus* indicates a fresh-water stage in its evolution. But many animals that have presumably always been marine, such as the Polychaeta, have functionally similar organs.

euchordates need not have been earlier than this free-swimming pre-urochordate. The first question to be discussed is whether it need have been later, whether in fact the two groups must have separated after the urochordates became sessile, so that we must admit a sessile stage in the ancestry of the euchordates in agreement with Berrill, who here follows Garstang.

Berrill's evidence for this conclusion is that he finds that "the primitive settling ascidian made and set the pattern of most of the chordate organisation not concerned with locomotion" (p. 124), in other words that many of the organs present in the settled ascidian, but not in the tadpole larva, find their homologies in the organisation of the euchordates. But the organs he discusses—the heart, the epicardium (which he believes homologous with the euchordate coelome) and the singe row of primary gill-clefts—are just those that we should expect to be present in the larger and better organised tadpole that we have concluded that the pre-urochordate ancestor would have been. Efficient circulation becomes more and more required as size increases; a space surrounding the viscera is a character found in all highly organised animals; and a number of gill-clefts is an obvious adaptation to efficient food collection as the pharynx grows larger. Finally, an atrium surrounding the body may have been evolved in this free-swimming animal for protection of the weakened body-wall in the region of the gill-clefts.

If these characters may have been evolved in the non-sessile pre-urochordate, they do not give us any real evidence of a sessile stage in the ancestry of the euchordates. For inescapable evidence of this we should need to find in the euchordate traces of organs which are adaptive to sessility but inadaptive to free-swimming life. If we found traces of the stalk, of the reduction of the nervous system to a cephalic ganglion, or of the forwardly directed atrial opening and anus, we could hardly avoid postulating a sessile stage. We find no such traces, and it seems to me that the claim for a sessile stage in the ancestry of the euchordate falls to the ground. I am sorry to have to come to this conclusion in disagreement with the great authority of Garstang.

Next we must consider the evidence that neoteny occurred in the ancestry of the euchordates. Neoteny is a term which has been used to cover phenomena of more than one kind, and it will be well first to distinguish its various uses.

One sense in which it is used is defined by de Beer (1940, p. 46) as a relative retardation of the development of the body compared with that of the reproductive glands—it might equally well be defined as a relative acceleration of the development of those glands—so that the organism becomes reproductive during development. This unquestionably occurs in living animals; we see it in the axolotl and de Beer gives other examples. To avoid using the same name for more than one phenomenon this may be called *paedogenesis,* a term that has often been used for it. Neoteny is also used for retardation of the development of any of the organs of the body if this results in the adult possessing characters present in related animals only during development. The embryonic characters of adult man are examples of this, and the larval characters of the perennibranchiate amphibians may well be another example. This is clearly a phenomenon distinct from paedogenesis. It has often been called *foetalisation,* but if this term is used it must be remembered that not all the characters involved are foetal.

In evolution foetalisation will produce resemblances between the young of the ancestor and the adult of the descendant; it will not have any further effects. Paedogenesis in evolution, if combined with loss of the original adult form, is supposed to produce effects that may be much more striking; a paedogenetic larva of which the adult has been lost is supposed to evolve and give rise to a new animal type. This is what Garstang sug-

gested in the origin of the chordates from a paedogenetic larva of a common ancestor of echinoderms and chordates, and Berrill believes to have been the process by which euchordates evolved from ascidians, the tadpole larva—or rather the ascidian at an early sessile stage of development—becoming paedogenetic and evolving by this, paedogenetic, type of evolution.

It has lately become fashionable to postulate paedogenetic evolution whenever the adult of one group of animals is found to resemble the larva of a related group. This is, first of all, to neglect the possibility of foetalisation. Even if foetalisation can be excluded, it is always very difficult to prove that the evolution has been paedogenetic; its occurrence is almost always purely hypothetical. I want to suggest that it is at most very rarely necessary to postulate evolution of this type, that almost all cases of resemblance between adults and larvae of related groups, if not due to foetalisation, can be understood on the lines of the general conceptions of the life-history outlined at the beginning of this section, and that no special hypothesis is necessary.

The origin of the euchordates provides an example of the type of explanation I put forward. I suggest that they were evolved, as were also the ascidians from the free-swimming pre-urochordate adult ancestor which possessed heart, epicardium, primary gill-clefts and atrium. The ascidians have been greatly altered by adaptation to sessile habit; the euchordates retain many more of the ancestral characters, since their mode of life has not been so radically altered. Similar explanations will cover many other cases where paedogenetic evolution has been suggested. For instance, de Beer (1940, p. 55) suggests that the insects may have arisen by paedogenetic evolution from a larval myriapod, since the larvae of some myriapods have the insect type of segmentation and tagmata, and resemble insects in other ways. Surely, it is more probable that both groups arose from common ancestors having these characters, that the insects have retained them and the myriapods modified them, e.g. by multiplication of the segments.

Paedogenetic evolution is a *possible* type of evolution, and the assumptions required for it are not in clear contradiction of our knowledge of the evolution of the life-history. It *may* have occurred but, where we have no direct evidence of its occurrence, I think we should not postulate it unless we are forced to do so by inability to explain the course of evolution in more normal ways. We cannot have direct evidence unless the characters of the adult ancestors are known, which they can be only if we have fossil evidence. I do not think that any supposed case of paedogenetic evolution is so supported. Perhaps, the origin of the Larvacea provides the example in which it is most difficult to find an explanation other than evolution by paedogenesis, for their resemblance in all their structure to tadpole larvae is very striking. But even here the evidence is not convincing; their origin may have been by simplification from the adult rather than by paedogensis from a larva.

I suggest then that neither a sessile stage nor paedogenetic evolution need have occurred in the ancestry of the euchordates. It seems to me that they arose by direct evolution from the free-swimming pre-urochordate stock which it seems necessary to postulate. I suggest also that this early stock gave rise by radiation, which we know to be a common phenomenon in evolution, not only to the ascidians and euchordates but also to the other groups of the Urochordata. The descendents of this stock would then be:

1. The Ascidiacea by adaptation to a sessile habit.

2. The Thaliacea by loss of the tadpole larva and tail, and use of the atrial current directed backwards as a means of locomotion.

3. The Larvacea by simplification or possibly by paedogenetic evolution.

4. The Euchordata by evolution of metameric segmentation giving more ac-

tive powers of locomotion and by other changes.

The phylogeny of the Chordata offers many problems not here discussed. Two are their connection with the echinoderms,[2] and the position of the Cephalochordata in the scheme—how far they are primitive and how far degenerate. It is not possible to discuss these questions in a short paper. It seems to me that the scheme I have put forward is preferable to that which Berrill advocates in that, while, as I believe, it satisfactorily accounts for the facts, it is more in accord with our general conceptions of evolution in animals, and asks for no *ad hoc* hypothesis of evolutionary process. It is not by any means original; it may in fact seem old-fashioned in being not far from that proposed by W. K. Brooks (1893) sixty years ago. I do not regard that as a criticism. To my mind the most recent ideas are not for their novelty necessarily to be preferred.

[2] I should, however, like to say that paedogenetic evolution seems to me no more necessary here than in the origin of the euchordates. Echinoderms and chordates may well have radiated from an earlier, non-sessile ancestral stock by direct modification of the adult.

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G. S. CARTER is a Fellow of Corpus Christi College and Lecturer in Zoology, Cambridge University. Dr. Carter will be remembered by readers of SYSTEMATIC ZOOLOGY for his recent discussion of Hadži's phylogenetic interpretations (1954, *3*:163–167, 173).

The Name *Psammochares* versus *Pompilus*

(*Concluded from page 155*)

of the hymenopterists signing or indicating agreement with the petition either were uninformed in regard to this case or did not have their wits about them at the time. None realized that he was requesting a sphecid to be the type of a genus to be made a *nomen conservandum* in the Psammocharidae, and none made investigations. Haupt signed the petition even though he had only the year before, in his monograph of the European Psammocharidae, stated that *Sphex viatica* Linnaeus is not a psammocharid but a sphecid: ". . . *Sphex viatica* L. ist kein *Pompilus* sondern=*Psammophila hirsuta* Scop., die jetz *Ps. viatica* L. heissen muss. Auch Dahlbom verstand diese Art darunter (vergl. Exercit. Hym. III 1832 p. 43 n. 21!)." (Before the Lisbon meeting in 1935, someone had noticed this and the type species of *Pompilus* in the request before the Commission had been changed from *Sphex viatica* to *Pompilus pulcher*.)

Of those signers who later made major contributions in this family (Haupt, Arnold, Pate, and Bradley), all except Bradley ignored or repudiated the petition, and used the names *Psammochares* and Psammocharidae in preference to *Pompilus* and Pompilidae. It is evident that such group actions are not necessarily the better way to arrive at sober and lasting decisions on problems of nomenclature, as under conditions usual to group actions even experienced authorities sometimes advocate actions that do not conform with their more carefully considered opinions.

It must be agreed that "cooperative decisions" as well as "individual decisions" can be and sometimes are, mistaken. When mistakes from either source are found, it is best that they be corrected.

HENRY TOWNES is at the Museum of Zoology, University of Michigan. He is working on monographs of Nearctic Ichneumonidae (Hymenoptera) under a grant from the Dow Chemical Company.

Points of View

The Ending for Subtribal Names in Zoology

Some families of animals, particularly among the insects, contain hundreds or even thousands of genera, and tens of thousands of species. In many such families, a need seems to be felt for additional taxal steps between the subfamily and genus levels, a need only partly met by the now familiar category of tribe. Formal subtribes are now solidly established and much used in the literature of some groups, e.g., the Carabidae and Staphylinidae (Coleoptera), and some families of Hymenoptera. There is perhaps a good case to be made against the establishment of more new *formal* categories between tribe and genus, and I for one would find it difficult to argue against some more informal and flexible kind of subdivision.

Nevertheless, the formal subtribe seems to be here to stay, and therefore we ought to give it proper attention in developing taxonomic methods and rules. The subtribe would, I think, require no more than routine attention were it not for one thing: the ending *"-ina."* This ending has caught on, at least among entomologists, and some want its use formalized through the Rules.

The terminal *-ina* is in my estimation an unfortunate choice; I shall now take up some reasons why. In the first place, *-ina,* is also the ending for a large number of generic names, so that a subtribal name with this ending, whether read or heard spoken, is not automatically distinguished as a subtribe, instead of as a genus or subgenus. Secondly, when spoken in several of the commonest languages or regional accents of these languages, subtribal names would be difficult to distinguish from the *-inae* ending for the subfamily or the *-ini* ending for tribe. Already, the similarity of *-inae* and *-ini* as pronounced by many speakers has caused confusion to listeners. Thirdly, we must recognize that vernacular forms based on the formal ones, now very useful when writing in common languages (e.g., French and English vernacular endings *-ine, -ines*) would have their associations distributed over three levels, instead of the present two (subfamily, tribe). The purpose of the ending, I take it, is to identify the level of the taxon. If the endings for different taxal levels are not sufficiently distinct, both in writing and in speaking, in formal as well as vernacular usage, then the endings do not serve the purpose. The confusion already raised by the similarity of *-inae* and *-ini* is regrettable, but these endings have now become so solidly fixed in usage that we probably have to live with them and continue to add some distinguishing term to the context so that we can tell them apart in practice. But the threat to clarity posed by the addition of a third scarcely distinguishable category, and one which furthermore is hardly separable in some situations from the genus category, is serious enough to call for the consideration of an alternative ending for the formal subtribal name.

It may be as well to mention here the schemes proposed by Stenzel and by Hubbs (see *Copenhagen Decisions on Zoological Nomenclature,* London, 1953, pp. 33-36), which seek to set up standard endings for a number of categories between family and genus. While the intentions behind these proposals are perhaps praiseworthy, the actual endings themselves as so far set forth are in large part subject to the same difficulties that I have mentioned as besetting the *-ina* ending. Adoption of either of these sys-

tems would just about preclude the use of vernaculars based on the formal names.

Without giving the matter much thought, I have in the past used the ending *-iti* for subtribes, and now it seems to me that a strong argument can be made for *-iti* as a better alternative to *-ina*. In the first place, *-iti* is the ending for extremely few generic names, most of which must be based on barbarisms or formed as anagrams. Offhand, I cannot recall a single generic name with the ending *-iti*, although a number with *-ina* endings come to mind instantly. Secondly, *-iti* is not easily confused, either written or spoken, with the endings of other taxa at and below the family level and above the species level. Thirdly, the *-iti* ending is readily transformed into a distinctive vernacular ending (French and English -ite, -ites) that will serve to prevent confusion in the less formal kinds of written or oral discussion.

I am not prepared to enter into arguments about the classical uses of *-iti*, or its present suitability on the basis of these uses. However, it is anticipated that *-iti* will be found sufficiently consistent with both classical usage and modern nomenclatorial requirements.

W. L. BROWN, JR.

Museum of Comparative Zoology
Harvard College
Cambridge, Mass.

Transliteration of Greek Words

In Section F of the Second Schedule of the proposed amended Rules a table is given to indicate the manner in which Greek words should be transliterated. The unofficial version issued by the Society of Systematic Zoology contains an error, in that the *iota* subscript has been omitted from the letter *omega* in the fourteenth example. The letter *omega* is, of course, transliterated as "o," and the improper diphthong as "oe."

It is unfortunate that the example illustrating the transliteration of the final *eta* should employ a word which was latinised in classical times as *Pirene*, and was never inflected in the first declension. It is scarcely less distressing that "Hippocrena, not Hippochrenes" should have been chosen to illustrate the transliteration of *kappa*, since this name was apparently known to the literary world of Rome only as *Hippocrene*.

It is always advisable to ascertain whether a particular Greek word was adopted into the Latin language in classical times. The Latin form can then be used with the assurance that it is in strict conformity with Article 3 of the Rules. One reason for this hint is that proper names were frequently adopted without transliteration of the final letter (*Phyle, Phylace*), technical terms with the minimum of change, and common names with full transliteration (*phylaca*). The simplest criterion in this matter is that if a word is listed in a standard Latin lexicon as having been used as part of the language, then it is a Latin word, and the onus of transliteration does not fall on its user. This criterion validates the use of such words as *oxalme, paramese, cataclysmos, parelion, parergon,* and *hepatizon,* all of which contravene the recommendations for transliteration cited in Section F. Rome adopted a wide assemblage of technical terms from the Greek, with the result that a word like *"parelion"* was just as much a part of the Latin language of classical times as "parhelion" is of current English.

R. G. FENNAH

Imperial College of Tropical Agriculture
St. Augustine, Trinidad, B. W. I.

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